An Investigation of Douglas-Fir Leave-Tree Mortality in the Sub-Boreal Spruce Zone: A Temporal Assessment of Water Relations Under Pre and Postharvest Conditions

Bruce J. Rogers

B.Sc., University of Northern British Columbia, 1998

Thesis Submitted In Partial Fulfillment Of

The Requirements For The Degree Of

Master Of Science

in

Natural Resources and Environmental Studies

(Forestry)

The University of Northern British Columbia

December 2006

Your file Votre référence
ISBN: 978-0-494-28429-2
Our file Notre référence
ISBN: 978-0-494-28429-2

An investigation of Douglas-fir leave tree mortality in the sub-boreal spruce zone: a temporal assessment of water relations under pre and postharvest conditions

Abstract:

Mature interior Douglas-fir (*Pseudotsuga menziesii var. glauca* [Beissn.] Franco) leave-trees show inconsistent survival when retained after harvest in the Sub-Boreal Spruce biogeoclimatic zone of British Columbia. Government policy is to maintain appropriate levels of leave-trees on cut blocks to meet biodiversity objectives. Douglas-fir is retained because populations are naturally fragmented at the northern edge of their natural distribution. In natural disturbance regimes dominant and veteran Douglas-fir trees that survive fire persist to ages of 300 to 500-years while new cohorts of spruce, lodgepole pine, and sub-alpine fir come and go beneath them, which make Douglas-fir ecologically appropriate candidates for leave trees. In 2002, data were collected which provided knowledge on the geographical range of leave tree mortality in the central interior and revealed factors potentially related to mortality. Subsequently, in 2003, potential changes in water relations around large and/or old, pre and postharvest Douglas-fir leave-trees were measured on typical Douglas-fir leave-trees in harvested and unharvested treatment units on two sites: harvested winter 2003 and harvested winter 1998. Twig water potential, soil moisture, and climate data suggest differences in water relations between treatments and sites. Sample trees in harvested treatments, in some instances, reach water potentials that may be lethal on more occasions than those in the unharvested treatments. It appears some trees may acclimate to their new environment after a few years. Stable carbon isotope ratio trends seen in 2004 suggest that the postharvest survival of a

percentage of residual trees on sites recently harvested may be diminished. To optimize the survival of Douglas-fir retention trees and to meet long term landscape level biodiversity objectives in the central interior, operational recommendations are to leave them either in untouched clumps of pure Douglas-fir or of mixed species rather than as single trees to maintain a suitable micro environment around the trees.

Table of contents:

List of tables:

List of Figures:

Glossary:

BEC: Biogeoclimatic ecosystem classification system of British Columbia.

Carbon isotope discrimination ($\Delta^{13}C$): Under non water stressed conditions during gas exchange, C3 plants assimilate less (discriminate against) of the heavier molecule ^{13}C through stomata in favor of the lighter molecule ^{12}C.

Cavitation: The breaking apart of the water column in a plants xylem tissue due to excessive transpirational pulling.

Ectomichorizal fungi: Soil fungi that have a symbiotic relation ship with plants, sharing water and nutrients by attaching to the external portion of the fine root tips.

Embolism: An air bubble that forms in plant xylem tissue as a result of cavitiation causing physiological damage.

Hydraulic resistance: Forces such as gravity and friction act against water that is drawn up through vascular tissue.

Hydraulic sufficiency: Equalization of the sufficiency of water transport e.g. tall conifers have reduced leaf area/sapwood ratios to avoid xylem cavitation when transpirational demand exceeds the sufficiency of the water delivery system.

Leave-tree retention system: A silvicultural system where single trees are retained on otherwise clearcut areas. Douglas-fir at its northern extent is often left on cutblocks to meet provincial biodiversity objectives. However, other silvicultural systems where single trees are retained for regeneration purposes are seed-tree and shelter-wood systems.

Sapwood: The newly formed outer wood located just inside the vascular cambium of a tree trunk and active in the conduction of water.

SBS: Sub-boreal spruce biogeoclimatic zone of British Columbia (see BEC)

Stable carbon isotope ratios ($d^{13}C$): The ratio of $^{13}C/^{12}C$ assimilated into plant tissue. During times of plant water stress the duration of stomatal closure increases and fixation of atmospheric $^{12}CO2$ decreases allowing for higher levels of the heavier $^{13}CO2$, already assimilated into the plant in relation to $^{12}CO2$ to be incorporated into plant tissue.

Stomata: Tiny pores in the epidermis of a leaf or stem through which gases and water vapor are exchanged.

Stomatal conductance; Movement of water through stomata to the atmosphere.

Turgor pressure: The pressure within plants cells derived from osmotic pressure differences that makes them rigid.

Vapor pressure deficit (VPD): Vapor pressure is the pressure exerted by a vapor in equilibrium with its liquid or gas phase. VPD is the difference between the vapor pressure within a plant's xylem and that of the atmosphere. VPD determines the transpirational gradient in plants and is a function of barometric pressure, temperature and relative humidity.

Water potential: Water potential is the tendency of water to move from an area of higher concentration to one of lower concentration. The rate at which transpiration is taking place in relation to water supply in plants results in a tension in the water column. When twig water potential is assessed it provides a measure of the water tension in the xylem, which when excessive can indicate water stress.

Water relations: Plant 'water relations' describes all of the aspects of water use by plants. This includes water potential in plants in relation to transpirational demand (negative water potential), the tendency for soil to hold water (gravitational, osmotic and matric water potential), and how the plant physiologically regulates water uptake and loss.

Water stress: Water stress occurs when the demand for water exceeds the available amount during a certain period restricting its use.

Xylem: Transport tissue found in vascular plants, whose main function is to conduct water and dissolved mineral nutrients from the roots to other parts of the plant where water is ultimately lost by transpiration from the leaves.

Acknowledgements:

UNBC graduate committee:

Dr. Chris Hawkins, Mike Jull, Dr. Kathy Lewis, Sue Grainger and Dr. Pranesh Kumar (Dr. Vic Lieffers)

Funding sources, technical advisors and project supporters:

Forest Science Program (FRBC, FII, FSP), John Prince Research Forest (Fellowship Award and in-kind), Science Council of British Columbia (GREAT Scholarship), Canfor (In-kind contributions), Winton Global (In-kind contributions), UNBC Mixedwood Ecology (In-kind and cash contributions), Aleza Lake Research Forest (In-kind contributions)

Dr. Peter Jackson (UNBC), Dr. Lito Arocena (UNBC), Dr. Mike Rutherford (UNBC), Dr. Darwyn Coxson (UNBC), Dr. Art Fredeen (UNBC), Dr. Hugues Massicotte, Dr. Scott Green (UNBC), Dr. Robert Guy (UBC), Dr. Peter Marshal (UBC), Dr. Barbara Bond (OSU), Dr. Dick Waring (OSU)

Gord Dow (MoFR), Craig DeLong (MoFR), Rick Fahlman (MoFR), Keith Gordon (MoFR), Ken Hodges (MoFR), Doug Becket (MoFR), Emile Begin (MoFR), Bob Brade (MoE), Joanne Vinnedge (MoE), Chris Ritchie (MoE), Dave Stevenson (MoE), Rhonda Thibeault (ILMB)

Peter Forsythe (Winton Global), John Elmsle (Winton Global)
Vince Day (Canfor), Steve Jenvey (Canfor), Steve Thorpe (Canfor)
John Marschelle (Apollo Lumber), Dennis Farquharson (Tolko Industries), Ken Day (Alex Fraser Research Forest)

Field assistants and project support staff:

Bob Madill (UNBC), Katie Krc, (UNBC) Cindy Baker (UNBC), Jennifer Lange (UNBC), Nicole Balliet (UNBC), Tracy Murray (UNBC), Jason Hutchinson (UNBC), Kim Menounos (UNBC), Adrian Batho (UNBC), Steve Storch (UNBC), Orrin Quinn (UNBC), Scott Scholefield (UNBC) Mark Stienen (UNBC)

1.0 Introduction

Interior Douglas-fir (*Pseudotsuga menziesii var. glauca* [Beissn.] Franco) reaches its northern range limit in regions of British Columbia (BC) that are transitional between the dry warm climatic regions of the central interior plateau, where Douglas-fir can form the dominant forest cover; and, the moist cold climatic regions of the sub-boreal plateau, where lodgepole pine (*Pinus contorta,* Dougl. Ex Loud), trembling aspen (*Populus tremuloides,* Mischx.) and white spruce (*Picea glauca,* Moench Voss) form the dominant cover (DeLong, 1999). The natural occurrence of Douglas-fir in many stands is primarily a consequence of wildfire (Herman and Lavender, 1988). Douglas-fir persist through wildfires because of their thick corky bark (Delong, 1999) and their capacity to form adventitious roots (Herman and Lavender, 1988). Thus in natural systems they are retained as veterans and naturally create two to three age class stands which provide diverse stand structure important as wildlife habitat (Grainger pers. comm. 2006).[1]

Historically, forest ecosystems in central British Columbia have experienced frequent wildfires that ranged in size from small spot fires to conflagrations covering tens of thousands of hectares (BC Ministry of Forests, 1995). Natural burns usually contained unburned patches of mature forest. Consequently, these forests produced a landscape mosaic of even-aged regenerating stands ranging in size from a few to thousands of hectares and usually containing mature forest remnants (BC Ministry of Forests, 1995). The presence or absence of Douglas-fir does not influence the disturbance frequency, but

[1] Grainger, S. 2006. Manager: John Prince Research Forest. Fort St. James, British Columbia.

determines the number and size of mature remnant stands that survive extensive crown fires (Herman and Lavender, 1988) to provide structural diversity. The current mountain pine beetle outbreak has accelerated cutting in pine-fir stands and has resulted in more Douglas-fir leave-trees on the landscape (Hawkins pers. com. 2005)[2] and the potential for more Douglas-fir leave tree dieback. This causes a concern amongst habitat managers who recognize the structural value of large, old, fire resistant Douglas-fir at its northern extent where these stand types are relatively rare.

Current government policy in the central interior of British Columbia states that maintaining structural attributes on the landscape associated with old forest that provide unique wildlife habitat is a priority (BC Provincial Government, 2002). Since the mid to late 1990's BC Ministry of Forest's policy has been to maintain large, old Douglas-fir trees after timber harvest to meet biodiversity objectives (BC Ministry of Forests, 1999). Douglas-fir provides valuable wildlife habitat such as critical winter range for mule deer at the northern extent of its range (Whittaker, 1996). In many areas at the northern limit of Douglas-fir's range, the geographic distribution of these fir populations are naturally fragmented (DeLong, 1999). Thus, local forestry practitioners implement prescriptions that attempt to emulate the type of forest structural retention that would occur as a result of natural disturbance such as wildfire. Although forest companies presently include Douglas-fir retention in their silvicultural systems, the prospect of high levels of subsequent mortality raises questions regarding the long term survival of these leave-trees.

[2] Hawkins, C.D. 2005. FRBC-Slocan Mixedwood Ecology and Management Chair Ecosystem Science and Management Program University of Northern British Columbia.

Low rates of Douglas-fir leave-tree survival in areas of the SBS have led some to question the ecological viability of partial cut Douglas-fir retention systems. In order to maintain biodiversity in managed stands, forest managers need to know how to preserve acceptable levels of live, postharvest leave trees in numbers that are felt to be similar to those present after natural disturbances. Improved knowledge of the expected performance of retention systems in relation to variable ecological conditions and natural disturbance regimes would allow for more effective stand, forest, and landscape level planning. The retention of mature Douglas-fir as a management biodiversity strategy has become increasingly important as forest managers seek to meet legislated biodiversity objectives following salvage harvest of pine stands killed by the current mountain pine beetle epidemic. This study addresses our lack of ecological understanding of factors affecting the viability of Douglas-fir leave-tree silviculture systems in central BC within the SBS. The aim of this research is to provide information to assist foresters and habitat biologists in central BC in meeting Douglas-fir management objectives for biodiversity and wildlife.

In 2002, I undertook investigations in the Prince George Forest District of central British Columbia focused on describing characteristics of typical Douglas-fir leave-trees, stand level variation in mortality rates, and documentation of site characteristics possibly associated with mortality. In 2002 no obvious site factors were observed that could be directly linked to tree mortality, and due to observed drought symptoms in Douglas-fir leave-trees it appeared water relations were impacted by logging, thus the focus of the study was directed at possible pre and postharvest changes in water relations.

Data collected during initial investigation in 2002 were examined to determine if trends in mortality existed in relation to site factors on cutblocks. However, due to the potential complexities of determining the actual primary mode of tree death (Table 1.1), this approach was supplemented and eventually replaced with other investigative approaches. Thus, the decision to pursue water relations as a study parameter was made. Many plants operate close to the hydraulic limits of transport, and cavitation of the xylem under excess tension can cause a rapid loss of conducting capacity and tissue mortality (Sperry et al. 2001). Therefore, increased stress on leave-trees due to changes in water relations as a resulting from canopy removals may be sufficiently detrimental to some, resulting in direct or indirect mortality.

Water relations and differences in local hydrology and microclimate between pre and postharvest conditions may play a role in the mortality of Douglas-fir leave-trees in the Sub-boreal spruce (SBS) Biogeoclimatic (BEC) zone of British Columbia (BC).

The central working hypothesis of this study is that postharvest changes in hydrology and transpirational demand will have adverse effects on the survival of large old Douglas-fir leave-trees. Related study objectives included the investigation of:

1) the extent and variability of Douglas-fir leave-tree mortality on cutblcoks in the Prince George TSA and the potential relationship between mortality and specific site factors;

2) whether trees in harvested treatments endure potentially damaging water stress levels for a greater period of time throughout the growing season than those in the unharvested treatments;

3) whether differences in microenvironment such as vapor pressure deficit (VPD) and soil moisture characteristics exist between trees in the harvested and unharvested treatments; and

4) how Douglas-fir retention policies and guidelines have evolved over the last 7 years, and what the implications around current policy and guidelines are for maintaining mature Douglas-fir as a component of future stands.

The premise of this approach is that local hydrology (water relationships) is significantly influenced by harvesting, and that single residual trees are thus impacted. Tree stress alone, if sufficiently severe, prolonged, or repeated, can cause continued or repeated dieback and even death (Houston, 1990). The extent of tree injury due to stress often depends on the duration of time it is exposed to the stress (Decoteau, 2005). Trees in both the unharvested and harvested units are likely to reach high levels of water stress under extremely demanding conditions. However, those in the harvested unit are expected to experience these conditions more frequently and possibly to a greater degree than in the unharvested unit. It is also expected that the postharvest micro environment around the leave-trees will be considerably different from pre harvest conditions.

1.0 Tables and figures:

Table 1.1. Potential confounding factors for determining single cause when measuring leave-tree mortality.

Possible contributions to mortality
1. Reduced soil pore space through compaction-fine root dieback
2. Mechanical and physical stress due to wind leading to imbalances of carbon allocation on some trees to compensate (H/D ratio) with increasing demand
3. Increased soil temperature and root respiration
4. Frost driving into fine root depth during winter harvest
5. Presence of pathogens e.g. Tomentosus root rot in some trees and bark beetles
6. Root grafting-removal of grafted tree with remaining tree still supporting stump and root tissue
7. Postharvest disproportions between shade-leaves and sun-leaves
8. Douglas-fir bark beetle
9. Excessive water surplus in harvested area due to decreased stand transpiration
10. Increased bole temperature

2.0 Literature review

2.1 Autecology/Silvics of Douglas-fir

Worldwide the *Pseudotsuga* genus is made up of 8 species; two of which are native to western North America and 6 to eastern Asia. The species native to Canada has two varieties; a coastal form *var. menziesii* and an interior form *var. glauca* (Farrar, 1995). Interior Douglas-fir is slower growing and less important commercially than coastal Douglas-fir. It grows up to 40 m in height and often exceeds 300-years of age (Farrar, 1995).

The elevation at which Douglas-fir are found in North America/British Columbia increases from north to south, reflecting the influence of latitude and climate on the distribution of the species. The environment of mid to low elevation Douglas-fir populations at northern limits are similar climatically to populations at higher elevations in the south (Hermann and Lavender, 1988). The principal limiting factors for growth and establishment are temperature at the north of the range and moisture in the south (Hermann and Lavender, 1988). Consequently, Douglas-fir is found mainly on relatively warmer southerly slopes in the northern part of its range, and on relatively cooler northerly exposures in the southern part. It is most commonly found on coarser well drained soil deposits or where bedrock occurs close to the soil surface (DeLong, 1999). At high elevations in the southern Rocky Mountains, however, Douglas-fir grows on the sunny slopes and dry rock exposures, mostly at elevations between 1830 and 2590 m

(6,000 and 8,000 ft), (Hermann and Lavender, 1988). DeLong (1999) compared two 14,000 ha areas, one in a drier warmer BEC unit (SBSdw3) and one in a wetter cooler unit (SBSwk1), and found that the distribution of Douglas-fir in terms of aspect and slope, typically showed the greatest abundance on south westerly slopes greater than 20% at mid elevations. The effect of slope and aspect was more pronounced in the wetter, cooler SBSwk1 subzone. Douglas-fir generally does not tolerate extreme drought conditions or waterlogged soils as well as other species such as Ponderosa pine (*Pinus ponderosa* P. Laws. ex C. Laws.) (Kanaskie et al. 1999). It has a low tolerance to high water tables (Klinka et al. 2000), where it forms plate like root systems to minimize inundation (Hermann and Lavender, 1988). Relative root biomass also decreases with age and may vary from 50 % at age 21 to less than 20 % in stands older than 100-years (Herman, 1985) and the size of the root system appears to be related to the size of the crown (Herman and Lavender, 1988). Root grafting is very common in stands of Douglas-fir, often leading to a system of interconnected roots in older stands (Lanner, 1961). Ectomycorrhizal fungi may also be important to Douglas-fir. Ectomychorrhizae associated with paper birch (*Betula paperifera* Marsh.) in plantations appears to reduce the incidence of *Armillaria ostyae* (Romagn.) Herink. rootrot, and improve both the nitrogen and pH status of the soil (Jones et. al, 1988).

2.2 Water relations

2.2.1 Drought stress

The term stress in biological science is often used for any environmental condition that is potentially unfavorable to living organisms for normal growth and development (Decoteau, 2005). Stressed plants may show a physical response (e.g. bending of a stem) or a chemical response (e.g. shift in metabolism). Stressing plants almost always has the suggestion of causing possible injury, and the plant may be severely injured or die if the stress is sufficiently severe (Decoteau, 2005). Drought has also been cited as the most important stress factor associated with declines of forests in the southern and southeastern United States (Houston, 1990).

Plant stomata act like a pressure regulator in water relations: sensitive to potential stresses and available soil water in relation to transpirational demand. A pressure regulator limits changes by controlling flow rate, and the stomata limit the variation in plant water potential with soil moisture and evaporative demand by controlling the transpiration rate (Sperry et al. 2002). Given the pressure regulator mode of stomatal function, it is inevitable that changes in hydraulic conductance of the soil-leaf pathway, soil moisture, and evaporative demand will indirectly drive changes in stomatal conductance and transpiration (Sperry et al. 2002). Water flow from soil to leaf cells is driven by water potential gradients, and leaf water potential is in equilibrium with guard cell water potential. The total flow rate from the soil to leaf unit area is the result of the

difference between soil water potential (less negative) and guard cell water potential (more negative) and a conductance coefficient termed soil-leaf-conductance (Gao et al. 2002). Water loss by transpiration is driven by VPD (vapor pressure deficit) and stomatal conductance (Gao et al. 2002). Increases in photosynthetically active radiation (PAR) induces increases in potassium cation concentration in guard cells, so that osmotic potential of guard cells decreases and that of the subsidiary cells increases (Gao et al. 2002). Thus, if increases in PAR are excessive, stomata will close to conserve water. Midday stomatal closure is mediated by soil water potential and the availability of water in the leaf and atmosphere (vapor pressure) (Bond and Kavanaugh, 1999).

Research has been extensive on plant response to water stress (Salsbury and Ross, 1978). The research has shown that as stress increases cellular growth and protochlorophyl production decrease, levels of abscisic acid, partially responsible for stomatal closure, increase, and respiration, translocation of assimilates and CO_2 assimilation can decline to almost zero (Salsbury and Ross, 1978). Drought stress always restricts the growth of trees (Tyree and Sperry, 1988). The immediate factor most influencing growth response to drought is turgor pressure (Salisbury and Ross, 1978 and Tyree, 1989), which is the force causing plastic enlargement of cells, leaves and stems. Reduced shoot and leaf growth in one dry season can reduce the vigor and growth potential of trees for several subsequent years (Tyree, 1989). Water stress might also upset the hydration of macro molecules. For example, this would include the water molecules that surround enzymes and nucleic acids. If this 'water of hydration' is upset, then plant function would be as well (Salisbury and Ross, 1978). The recovery time can vary greatly by species, with the

harmful effects of the drought sometimes lasting from weeks to months. This can occur if stomata are slow to regain their conductance, or photosynthetic machinery is damaged (Kozlowski and Pallardy, 1997).

Under severe drought conditions, water content may drop to a critical level where trees are irreversibly damaged and entire trees or just portions of the tree may die (Kanaskie et al. 1999). For example, dead branches, dead tops and dead Douglas-fir trees were unusually abundant and widespread during drought conditions in Oregon during 1999, particularly noticeable in the xeric interior southwest (Kanaskie et al. 1999). Tops of trees and branch tips often die first because they are farthest from the water-absorbing roots: the longest path for the water to travel. Even though the damage may occur in late summer or fall, the symptoms usually are not visible until late winter or the following spring (Kanaskie et al. 1999). Taller trees that are compromised hydraulically may compensate through foliar dieback. For example, there was considerable evidence of crown stress and dieback for large, old-growth canopy Douglas-fir trees at the Wind River Canopy Crane site, Carson, Washington, USA (Bauerle et al. 1998). Top dieback has also been observed in exotic species such as Norway spruce, and may be attributed to excessive moisture loss in winter (Redfern, 1991). The principle characteristics of top dieback conditions as described in Redfern (1991) are as follows: 1) basipetal browning of current years needles usually occurs during winter and early spring, but may begin as early as late summer, 2) growth reduction may be concurrent with browning and may even precede it, 3) the condition most commonly affects the pole stage, and 4) it is typically initiated by the removal of side shelter. Dieback of trees or tissues often results

from the effects of stress factors alone (Houston, 1990). A number of studies have identified hydraulic limits as the cause of partial or complete foliar dieback in response to drought. The regulation of plant water potential by stomatal control and leaf area adjustment may be necessary to maximize water uptake on the one hand, while avoiding loss of hydraulic contact with the soil on the other (Sperry et al. 2002).

Increasing tree height and drought present fundamentally similar challenges to tree function by reducing leaf and xylem water potentials which have consequences for leaf photosynthetic function (Tezara et al. 1999). Both of these factors also have similar consequences for vulnerability to xylem cavitation (Sperry et al. 1993). Spittlehouse (2002) found that older (>125-years) lodgepole pine trees with small crowns were subject to reduced hydraulic conductance between the roots and the leaves which can significantly reduce transpiration rates. Root source signals might anticipate tree stress in a general manner, and trees may not respond to specific cavitation events because the progressive failure of the xylem under a constant transpiration rate would at first have no effect on upstream root water potential (Comstock, 2002). Further, in the final stages where xylem conductivity has been lost entirely, root water potential would be more positive (Comstock, 2002).

Douglas-fir experiencing drought stress have stomata closed for longer periods than normal, thereby limiting gas exchange for photosynthesis. Changes in stable carbon isotope ratios ($d^{13}C$) due to carbon isotope discrimination ($\Delta^{13}C$) can be an indicator of drought stress. Photosynthesis by terrestrial C_3 plants discriminates against CO_2 with ^{13}C

relative to CO_2, with ^{12}C, because ^{13}C has a lower diffusivity through the stomatal pore and lower reactivity with the photosynthetic enzyme Rubisco (McDowell et al. 2002a). Under non limiting conditions, this discrimination results in a decrease in ^{13}C of plant matter of approximately 20 % below that of atmospheric CO_2 (McDowell et. al. 2002a). Although it is not possible to estimate exact fluxes of assimilated carbon during water deficit, carbon isotope discrimination represents an easy to use tool to study integrated plant adaptations to drought stress because the $^{13}C/^{12}C$ ratio does reflect variability under extreme conditions. (Arndt and Wanek, 2002). McDowell et al. (2004) found that consistent with stomatal conductance control over photosynthesis and $\Delta^{13}C$, foliage $\Delta^{13}C$ (ecosystem respired) became enriched as net CO_2 uptake decreased (more positive values).

Stable carbon isotope ratios have also been used to examine other modes of stress in Douglas-fir, such as that induced by dwarf mistletoe (*Arceuthobium spp.*) (Sala et al. 2001). Heavily infected Douglas-fir trees $d^{13}C$ showed significantly different values (e.g. more positive) than uninfected trees (Sala et al. 2001). Studies indicate significant, and potentially exploitable, intra-specific variation in a number of morpho-physiological (physiological structure) traits related to drought tolerance including rate of gas exchange, osmotic adjustment, and stomatal density (Sala et al. 2001). Moreover, another study has demonstrated that $\Delta^{13}C$ may be used as a surrogate to select for improved water-use efficiency in crops and trees (Farquhar et al. 1989). Carbon isotope discrimination ($\Delta^{13}C$), calculated from the $^{13}C/^{12}C$ ratio was used to show that leaf proportional phosphoenol pyruvate carboxylase (PEPcase) activities in *Salix interior*

Rowlee and *Nicotiana tabacum* L. plants decreased as $\Delta^{13}C$ increased, and that PEPcase activity was higher in younger more heterotrophic (carbon gained from import) stages than in older more autotrophic (carbon gained from photosynthesis) stages (Le Roux-Swarthout et al. 2000). Thus, a range of carbon source contributions in plant materials can be indicative of variable $\Delta^{13}C$. $d^{13}C$ values increased (became more ^{13}C enriched) in older versus younger Douglas-fir trees at two sites at the Wind River Canopy Station in Oregon (Bond, et al. 1999). After examining populations of *Pinus greggii* Engelm. ex Parl. in central Mexico, Garcia-G, et al. (2004) determined that the ^{13}C signature of wood (radial increment) provided a good integral index for screening populations of this species adaptation on dry sites.

2.2.2 Hydraulic limitation and tree physiology

Many Douglas-fir in the central interior of British Columbia may attain heights of more than 40 m and can potentially be much older than other species in the stands where they are found. Thus, large and/or old Douglas-fir trees may be functioning at the maximum limit of their hydraulic conductance (water movement thorough the tree from ground to atmosphere) potential due to changes in whole tree hydraulic conductance with increasing age and height (Ryan et al. 2000, Phillips et al. 2002, Ryan and Barnard 2003, Koch et al. 2004). If this were the case, sudden changes in moisture availability or demand may exert intolerable stresses on them. Philips et al. (2002) tested for reductions in water transport with increasing tree size in young (15 m tall, 21 years old), mature (32 m tall, 40-years old), and old Douglas-fir trees (60 m tall, 450-years old). The effects of

low soil water content on stomatal and hydraulic conductance were found to be most pronounced for the tallest (60 m) trees. This suggests some differential influence of soil water limitation with tree height. Reductions in stomatal or crown conductance have also been shown to be associated with increased hydraulic resistance (Philips et al. 2002). Studies have shown whole tree estimates of leaf-specific hydraulic conductance to be lower in larger, older trees than in smaller, younger trees in several species (Philips et al. 2002).

Gravity's effect on the water column may impede growth at the top of the crown in tall trees and may lead to branch and top dieback as the result of sheer height and hydraulic limitations (Ryan and Yoder 1997). Water transport in woody plants is limited by the hydraulic sufficiency of the xylem. When xylem water potential becomes sufficiently negative, cavitation occurs with air introduced into the tracheids or vessels forming an embolism (Crombie et al. 1985, Sperry and Tyree, 1990). Creation of an embolism in sapwood of a woody plant increases resistance to water flow resulting in stomatal closure (Sperry and Pockman 1993, Sperry et al. 1993), foliage loss (Kavanagh and Zaerr 1997), and eventually mortality (Tyree and Sperry, 1988) if the stress is prolonged (Decoteau, 2005).

Transpiration and plant water potential must be regulated to stay within specific physical limits related to steady-state transpirational rates in the soil-leaf pathway, or else canopy desiccation will occur (Sperry et al. 2002). The existence of hydraulic limit means that 'pulling' harder on the water column does not necessarily mean that leaves get more

water. Plants may need to regulate their rate of water uptake to stay within the hydraulic limits of the supply line (Sperry et al. 2002). Data from bole increment cores taken from Oregon white oak (*Quercus garryana* Dougl. Ex. Hook) suggest some compensatory changes in sapwood conductance such as higher sapwood porosity in taller trees may moderate some hydraulic constraints, but that this may not overcome limitations associated with overall hydraulic path length (Phillips et al. 2003).

Philips et al. (2002) supports the hydraulic limitation hypothesis proposed by Ryan and Yoder (1997): tree height growth and productivity decline as trees age because of stomatal limitations induced by increased hydraulic path-length resistance and gravity. The leaf area to sapwood area ratio has been hypothesized to decrease as trees become older and taller (Philips et al. 2002). Some theories suggest that this ratio must decrease to maintain hydraulic efficiency as path length, gravity and tortuosity (twistedness or crookedness) constrain whole plant conductance (Philips et al. 2002). To test this hypothesis, the whole tree ratio was measured on 15 individual Douglas-fir (*Pseudotsuga menziesii* var. *menziiesii*) trees ranging in height from 13 to 62 m (aged 20 – 400-years). It was observed that leaf area to sapwood area ratio declined substantially as tree height increased (McDowell, 2002 a). This trend was also observed in *Pinus ponderosa* (P. Laws. Ex C. Laws) and *Pinus sylvestris* (L.) (McDowell, 2002 b). The observed decrease in leaf area to sapwood area ratio with increasing tree size may be a homeostatic mechanism that partially compensates for decreased hydraulic conductance as trees grow in height (McDowell, 2002 b).

In an old growth (approx. 460-years) Douglas-fir and western hemlock (*Tsuga heterophyla* (Raf.) Sarge.) forest, dominants and saplings were compared for water potential or whole tree water relations at the Wind River Canopy Crane site, at Carson, Washington, USA (Bauerle et al. 1998). Lower stomatal conductances were observed in the dominant trees relative to saplings (Bauerle et al. 1998). It has been hypothesized that there are limits to the maximum heights that trees can attain and that these limits are most often set by stem hydraulic conductivity (Ryan and Yoder 1997, Koch et al. 2004). A progression of increasing hydraulic constraint with height has also been observed in Douglas-fir seedlings, saplings, and large trees, who react very differently amongst each other to both natural and anthropogenic stresses in terms of stem hydraulic conductivity (Samuelson and Edwards 1993, Grulke and Millier 1994, Kelly et al. 1995, Fredrickson et al. 1996, Kolb et al. 1997, Chapelka and Samuelson 1998).

2.2.3 Pathogens

Two agents of mortality for Douglas-fir in central British Columbia that may not be obvious in their early stages of development when carrying out ocular assessments from a distance are *Inonotus tomentosus* ([Fr.:Fr.] S. Teng.) root rot and Douglas-fir bark beetle (*Dendroctonus pseudotsugae*) (Henigman et al. 2001).

Douglas-fir bark beetle is often associated with mortality as a secondary agent when trees have been weakened by drought (Schmitz and Gibson, 1996, Henigman et al. 2001) and/or root rot (USDA Forest Service, 2006). Armilaria root disease (*Amillaria ostoyae*

[Romangb.] Herink) is associated with the mortality of many woody plant species including Douglas-fir in southern latitudes of the province. However, *I. tomentosus* is the root rot which Douglas-fir is moderately susceptible to at this latitude (Henigman et al. 2001). This fungus enters the small lateral roots killing the cambium of the main root on its way to the heart wood causing dysfunctional roots followed by growth reduction and mortality (Lewis, 1991).

Over 300 heart rot fungi are known to attack Douglas-fir. Red ring rot (*Phellinus pini* (Thore:Fr.) Ames) entering through knots and scars resulting from fire, lightning, and falling trees is the most damaging and widespread rot (Herman and Lavender, 1988). In 2003 *P. pini* fruiting bodies were observed on the lower boles of a number of Douglas-fir trees south of Prince George BC by the author. Other important heart rot fungi in the Pacific Northwest are *Fomitopsis officinalis* (Vill.:Fr.) Bond. & Sing, *F. cajanderi* (Karst.) Kotl. & Pouz, and *Phaeolus schweinitzii* (Fr.:Fr.) Pat (Hepting, 1971). In 2002 fruiting bodies of the latter species were observed on lateral roots of mature Douglas-fir in Fort St. James in central BC by the author.

Lack of water, or drought, does not normally cause pathological phenomena in naturally forested areas. However, during very long dry periods, conifers may die in groups, particularly on sites where soil is shallow and coarse (Hansen and Lewis 1997). Winter buildup of surface ice during cold, snow free spells may also cause drought in the soil and asphyxiation of roots that grow under an ice lens when the growing season begins (Jalkanen, 1997).

Aside from drought, soil conditions such as water surplus can also predispose trees to pathogens. The coincidence of adverse soil conditions with defoliation prevents the rapid transpiration of surplus water, thus prolonging adverse conditions for the root systems (Halmschlager, 1997). Weakened or damaged roots are more susceptible to aggressive pathogens that may be present (Halmschlager, 1997). Infections by pathogens that are initiated in such situations cause persistent disruption in the function of the root system and thus increases the susceptibility of the tree to other stress agents (Fuhrer, 1988). The combined effects of the exposure of trees to current and past environmental conditions have an influence on their predisposition to compounded pathological processes and mortality. Pederson (1998) observed 40 % mortality in Midwestern oaks over a 5-year period that was attributed in part to drought stress, and that tree mortality was associated with a combination of long-term stresses and infrequent, short-term stresses. For example, the long-term nature of the tree mortality process illustrates the difficulty of attributing tree mortality to one specific cause. In particular, attempts to assign one or more causes for the death of a tree based solely on the tree's current environment and condition will likely fail, or lead to incorrect conclusions (Pederson, 1998). Factors that influenced trees for decades prior to mortality must be considered if the causes of mortality are to be fully understood (Pederson, 1998).

2.3 Effects of harvesting on water relations

2.3.1 Changes in hydrology with harvesting

Increases in exposure of individual trees and stand edges created by logging increases canopy evaporative demand in residual uncut leave-trees as the sides of the canopy are now exposed to the atmosphere as well as the bole. Stress events such as drought initiate crown dieback, refoliation, seed production, defense, and possibly other energy demanding processes that limit growth of xylem transport tissues (Manion, 1997). Factors such as changes in soil moisture or hydrology are not likely the sole cause of Douglas-fir leave-tree mortality. However, it is hypothesized that it can be a primary tree stress factor after harvest. Reduction in xylem transport tissues as a result of stress events limits recovery of mature, dominant trees, resulting in further dieback and predisposition to invasion by organisms of secondary action (Manion, 1997). Thus, there may be cases where there is no single biotic or abiotic cause for death (Manion, 1997). Understory trees and younger trees may recover, while mature overstory trees preconditioned by highly demanding crowns dieback further because of decreased transport capacity (Manion, 1997). Competitive dominant trees are acclimated to depend on the annual production of xylem transport tissues to maintain a large crown in a closed canopy condition (Manion, 1997).

Although the Douglas-fir single tree retention system is essentially a clearcut with residual trees similar in some ways to that of a single tree retention seed-tree or shelter-

wood silivcultural system, it may still be thought of as a dramatic density reduction treatment in the context of water relations and hydrology. The positive growth response of healthy young trees to density reduction is well known. In contrast, large, old trees are usually thought to be intrinsically limited in their ability to respond to increased growing space; therefore, density reduction is seldom used in stands of mature trees (Latham and Tappeiner, 2002). Two hundred and seventy one Douglas-fir trees ranging in age from 158-650-years were examined 20-50-years after density reduction. Density reduction included either light thinning to remove less vigorous trees, or shelterwood treatments in which overstory trees were not removed. Ratios of basal area growth after treatment to basal area growth before treatment, and several other measures of growth, all indicated that the old trees sometimes benefited and were not harmed by density reduction (Latham and Tappeiner, 2002). Based on preliminary data and much in depth observation of postharvest density reduction in old Douglas-fir stands in the north central interior of British Columbia, there are indications that either the silvics of these trees or the impact of latitude and climate on the trees differs from the Oregon observations of Latham and Tappeiner (2002). Changes in water relations as a result of extreme density reductions, such as those seen on clearcuts with residuals, may introduce stresses that inhibit the leave-trees in our study from exploiting increases in growing space.

Deforestation results in diminished transpiration and increases in soil moisture content. In Lorraine, France, a reduction in evapotranspiration of 29 percent was observed after a forest was clearcut (IUFRO, 2002). Comparisons between the evapotranspiration of forests to that of grasslands may approximate that of newly harvested cutblocks. IUFRO

(2002) suggested evapotranspiration of forests is higher than that of formations of low height, such as grassland. When the water deficit increases, forests consume considerably more water than grassland, as their deeper rooting enables them to completely exploit the hydric reserves of the soil. However, under conditions of extreme drought their more efficient rooting system is no longer an advantage because the small amounts of precipitation cannot supply sufficient water (IUFRO, 2002). Whole-tree, clearcutting and progressive strip-cutting of northern hardwood forests at the Hubbard Brook Experimental Forest in central New Hampshire resulted in measurable changes in physical and chemical conditions of forest streams, demonstrating the impact that harvesting can have on stand level water use (Adams, et al. 1991). Martin et al. (2000) observed an increase in water yield of >150 mm for the first year after whole-tree harvesting, as a result of reduced transpiration and interception. The majority of which occurred during the growing season.

2.3.2 Soil changes and impacts on roots and available water

Plants can respond to soil conditions in ways that cannot readily be explained in terms of the ability of the roots to take up water and nutrients. Roots exposed to adverse soil conditions send inhibitory signals to the shoots (Passioura, 2002). The inhibitory signals may affect stomatal conductance, cell expansion, cell division and the rate of leaf appearance. Their nature is still under debate. The debate is becoming increasingly complex, possibly signifying that a network of hormonal and other responses are involved (Passioura, 2002). The range of soil conditions that produce such responses

includes: physical (hardness, dryness); chemical (hypoxia, salinity); and biological (initial infection by disease organisms) sources (Passioura, 2002). That plants have developed such responses if water supply is at risk seems a good evolutionary strategy, because once soil water potential has fallen to a level that directly affects leaf water potential there is typically so little available water left in the soil that the plant is in danger of severe wilting (Passioura, 2002). For example, when soil dries due to water deficit, many changes take place. It not only holds water more strongly, but it also becomes harder and transmits solutes less readily so a deficiency of poorly mobile nutrients such as phosphorous is more likely. Plants eventually respond to the falling water potential of their leaves by closing their stomata and slowing their growth (Passioura, 2002).

Water deficit is not the only factor associated with tree stress. Douglas-fir has low tolerance to water surplus (Klinka et al. 2000). Root mortality under the influence of continuous oxygen deficiency in heavy, water-saturated soils is reported frequently as a cause of dieback of oaks (Prpic and Raus, 1987, Varga, 1987, Hartmann 1996). In waterlogged or flooded soils, tree roots are deprived of oxygen and may be killed or damaged to the point that they can no longer absorb water and nutrients efficiently (Kanaskie et al. 1999). As the soil dries, the damaged root system cannot support the water needs of the top of the tree. Low levels of water stress reduce stem and root growth. As water stress increases, production of defensive chemicals decreases. This can increase a tree's susceptibility to certain insects and pathogens (Kanaskie et al. 1999).

Soil moisture levels during 1960-1980 were compared for two areas within a 101 ha watershed in the Oregon Cascade Range (Adams et al. 1991). In winter 1962-1963, the old-growth Douglas-fir forest in one area was clearcut. An adjacent forested area was left undisturbed as a control. In summer 1963, the upper 120 cm of soil in the clearcut averaged over 10 cm more residual moisture than in the forested control. By 1967, these surpluses in the clearcut had declined to become deficits of at least 2 cm compared to the control. The deficits, which were presumably caused by a rapid increase in plant cover after the light slash burn, persisted in the upper 30 cm of soil throughout the rest of the study. The observed fluctuations in soil moisture in the treated area are extensive enough to influence forest regeneration and watershed hydrology (Adams et al. 1991).

Excess water is also a recognized problem in undrained peatlands and mineral soils. After clearcutting the ground water level tends to rise (Jalkanen, 1997), generating several kinds of signals when roots are exposed to environmental stress (Jackson 2000). Some, but not all signals are conveyed to shoots in the transpiration stream (Jackson 2000).

Stout and Sala (2003) found that roots under water deficit were more vulnerable to cavitation than shoots in both Douglas-fir and ponderosa pine. Alder et al. (1996) proposed this may be an adaptive process if root cavitation in response to water stress limits water transport, thereby delivering a hydraulic signal to shoots that triggers stomatal closure. In many dryland species, flooding of the soil can also induce developmental responses in the shoot (Alder et al. 1996) such as epinastic leaf curvature

observed frequently on Douglas-fir leave-trees (Rogers and Hawkins, 2003), stomatal closure and slowing of leaf expansion. These reactions compensate for diminished input from the roots (Jackson, 2000).

Oxygen shortages and soil strength are major limitations to root growth (Coder, 2000). Tissue death and subsequent compartmentalization processes can compound mechanical faults (Coder, 2000). Growth regulation and carbon allocation changes can modify stem and root collar taper and reaction wood development (Coder, 2000). Top and root dieback as well as branch drop can be the result (Coder, 2000). As roots are put under greater than 1.2 MPa of pressure, elongation slows and stops (Coder, 2000). Trees begin to generate thick and short roots with many more lateral roots as surrounding soil pressure (water potential) exceeds 0.5 Mpa (Coder, 2000).

Root growth and function are severely compromised in compacted soils. Machine traffic across an area where trees are growing can result in the soil becoming denser and less accommodating to the movement of water and gases (Pratt and Schnelle, 2003). Huang et al. (1996) found that there was an increase in soil bulk density and a decline in hydraulic conductivity associated with logging due in part to a decrease in soil pore size and that the reduction in porosity suggests a reduction in aeration and a change in water retention characteristics. One possibility with implications for interrupted hydraulic conductivity in postharvest leave-trees is root dieback as a result of mechanical compaction and/or postharvest water surplus. Compaction-associated physiological dysfunctions cause systemic damage and decline, as well as failures in dealing with

additional environmental changes (Coder, 2000). Physical - mechanical constraints negatively modify responses in the tree resulting in inefficient use of essential resources (Coder, 2000).

Loss of overstory shading after harvest can lead to increased soil temperature that is associated with increased soil evaporation. Soil evaporation occurs when the atmospheric vapor pressure is low compared to the vapor pressure at the plant and soil surfaces. Increased temperature and wind result in an increase in vapor pressure at the plant and soil surfaces but have less effect on the atmospheric vapor pressure, thus, evaporation proceeds rapidly (Brady, 1990). The degree of shading of plant leaves known as leaf area index, significantly affects the radiant energy that reaches the soil surface, and in turn, the evaporation that takes place (Brady, 1990). Higher fine root mortality in a wide variety of coniferous and deciduous trees was observed during times of extreme soil temperature (Hendrick and Pregitzer, 1993 and Pregitzer et al. 1997). This may also be a factor that ultimately limits water uptake by Douglas-fir leave-trees under more demanding conditions. Douglas-fir fine roots, smaller than 0.5 cm in diameter develop mostly from smaller lateral roots and are concentrated in the upper 20 cm of soil (Herman, 1997) where they would be could be exposed to changes in temperature. They have a short life-span, ranging in general from a few days to several weeks. Fine root turnover changes seasonally, and is influenced by changes in environmental conditions (Santantonio et al. 1985).

Increases in soil temperature, were observed in experimental treatments with lower relative ground surface shading than an old growth and unharvested treatment (Grifiths and Swanson. 2000). Thus, surface soil evaporation would have also increased (Brady, 1990). Forest soil characteristics in a chronosequence of harvested Douglas-fir stands were examined in different climate settings. Included were an old growth control and 5, 15 and 40-year-old cutblocks. Soil moisture measurements showed no significant difference between the experimental units; however, this was tested using a gravimetric procedure as opposed to continuous sampling. Summer soil temperatures were found to be lower in the control and the 40-year-old stand than in the younger stands (Grifiths and Swanson. 2000). Increased soil acidification has also been observed following periods of increased soil temperature and decreased precipitation (Tomlinson, 1992). Soil acidification and leaching can result in the loss of available cations such as Ca^{2+}, Mg^{2+} or K^{+}. The cumulative loss of these cations, if greater than the amount released from the specific minerals in that soil, can lead to nutrient deficiency, fine root mortality, poor growth, and eventually to die-back (Tomlinson, 1992).

The spatially variable nature of Douglas-fir leave tree mortality on cutblocks may also be in part as a result of variable moisture availability on the site. Moisture stress can vary at the stand level because of variable soil moisture availability (Ministry of Forests, 2002). Variability of available moisture across the Pothole Creek silviculture study site in south central British Columbia affected regeneration success and overall tree growth, and interacted to some degree with the physical features of microsite and substrate (Ministry of Forests, 2002). Sap flow in Douglas-fir was measured to identify specific responses to

soil moisture variability. Spatial variation in moisture stress might have been caused by uneven snow accumulation and melt, grass evapotranspiration as related to leaf area and energy availability, soil depth and thus water storage variability, water use by large trees, and patterns of shade and light (Ministry of Forests, 2002). This illustrates the dynamics associated with changes in moisture and Douglas-fir stress.

2.4 Impacts of altered water relations on tree productivity and vigour

Clearcut harvesting of surrounding trees provides new dramatically different environments for trees that have adapted to conditions in undisturbed forests. For example, when clearcut forest boundaries were evaluated for their effects on mature and regenerating trees in the northern interior of British Columbia, Burton (2002) found that mature *Pinus contorta* trees on south facing slopes showed an unexplained 48% decrease in radial growth compared to average growth rates in forest interiors, an effect that was detectable up to 45 m into the forest. This growth reduction indicates loss of vigor in the affected trees.

It is theorized that large, old Douglas-fir trees in central BC may be limited in their ability to produce surplus energy reserves needed for vigorous response to sudden environmental changes following harvest of the surrounding stand. Although it is generally accepted that the stand level rate of biomass production decreases as forests age, little is known about the relative contributions of this decline to changes in net primary productivity (NPP) and tree mortality (Acker et al. 2002). Grier et al. (1989)

reported that the rate of biomass accumulation for *Pseudotsuga menziesii* forests in the Pacific Northwest peaks at about 20-years of age, even though this species often dominates stands for up to 500-years in the absence of disturbance (Franklin and Halpern, 2002). Although net primary production has been the subject of many short term studies, Ryan et al. (1997) assert that there are few long term studies that compare the relative contributions of changing production and mortality rates to long term trends of biomass accumulation. In a study that included Douglas-fir, both live and dead, bole biomass was computed (Acker et al. 2002). Biomass accumulation is the net result of productivity and mortality. The results of this study showed that a decrease in NPP (net primary production) and an increase in tree mortality both contributed to a decrease in biomass accumulation with stand age (Acker et al. 2002). The difference in NPP between the highest observed value for the young stand and the mean value for the old growth stands was -4 Mg/ha/year. Thus, the apparent decrease in biomass accumulation with stand age appears to be the result of a decrease in production and an increase in mortality (Acker et al. 2002). At the northern extent of their range, Douglas-fir as a component of spruce or pine leading stands are often the largest and oldest trees present. Bond et al. (1999) hypothesized that hydraulic resistance increases as trees grow and age, and that increased resistance results in lower rates of photosynthesis and transpiration in older trees, thereby reducing productivity in older stands. In the Bond et al (1999) study, leaf area: sapwood area ratios were used for "scaling up" the sapflow and gas exchange measurements. Sap flow was found to be much higher per unit area in younger trees and sap flux lower in older sapwood compared to younger sapwood.

In an alternative view of hydraulic limitations to growth, Magnani et al. (2000) proposed that allocation to fine roots compensates for increased hydraulic resistance above-ground, so that a constant level of hydraulic supply to the leaves is maintained at the whole-plant (not the shoot) scale during tree growth. The carbon cost of maintaining and replacing fine roots was found to be very large in mature trees, and enough to reduce forest NPP (Magnani *et al.* 2000). Thus, the suggestion is made by Becker et al. (2000) that the 'hydraulic limitation hypothesis' should be reformulated considering partitioning of dry matter above and below ground and the consequent carbon gains and costs in addition to considering structural changes and leaf area-sapwood area changes with increasing tree height. There may also be a height (stem diameter) threshold beyond which the maximum driving force begins to decline because the increasingly negative gravitational component of water potential acts to diminish the net driving force for water transport with increasing height (Meinzer, 2003). In general, a tree's stomatal regulation is aimed at preventing leaf or stem water potential from falling below a threshold minimum value associated with excessive loss of xylem function due to cavitation and the efficiency and integrity of xylem water transport is strongly related to variation carbon allocation and wood density (Meinzer, 2003).

Clearly, water relations of Douglas-fir trees are complex and when stressed, the potential negative outcomes are numerous. They range from stomatal closure, tissue death, infections by pathogens and tree death. The mechanisms underlying these phenomena are poorly understood. A better understanding of these mechanisms will assist forest managers in meeting their management objectives with respect to Douglas-fir leave trees.

3.0 Background: Forest policy and practice

At the start of this study (January 2002), the apparent problem or extent of Douglas-fir leave-tree die-back in the SBS had not been systematically documented or addressed. Field observations to date had been widespread, but largely anecdotal in nature (Jull, 1999). Up until 2002 many observations of mortality were attributed to Douglas-fir beetle, and root rots alone. However, upon closer examination it became clear that this was not always the case. Therefore, the need existed to better document the level and distribution of Douglas-fir leave-tree die-back across the SBS in order to support regional Douglas-fir management guidelines (BC Ministry of Forests, 1999).

The objectives of the Ministry of Forests regional Douglas-fir management guidelines (BC Ministry of Forests, 1999) are:

- No net reduction/loss of area of Douglas-fir leading, major or minor forest types in a landscape unit, which implies adequate regeneration of Douglas-fir after harvest, and,
- Retain a postharvest range of Douglas-fir stand structure and age classes representative of the range present in the pre-harvest conditions.

More specifically, the intent of the regional guidelines is to retain Douglas-fir leave-trees in a windfirm undamaged condition within areas harvested under operational plans. This includes: (1) adequate levels of large old Douglas-fir trees, either in individual-tree or

group reserves, and (2) adequate levels of a representative range of younger and older age class of residual Douglas-fir.

The revised BC Government Biodiversity Order of 2005 establishing landscape level biodiversity objectives for the Prince George Timber Supply Area established targets for percentages of areas of retained 'old forest' (> 120-year old forest stands) based on the current forest cover inventory. Much of the Douglas-fir in central BC is contained within the SBS dw2, dw3 and mk1 biogeoclimatic subzones (Delong, 2003). For the purposes of the Forest and Range Practices Act of British Columbia, all new forest stewardship plans must be consistent with the Order (BC Provincial Government, 2005). This order is enabled under the Forest and Range Practices Act (FRPA) and all new operational plans must address specified landscape-level retention targets (BC Provincial Government, 2005).

The Order acknowledges that due to the extraordinary situation of the mountain pine beetle epidemic in the Prince George TSA, it is assumed that there will be a deficit of live old forest in some units to meet the retention target's requirements. For this reason, these "non-live" old forests" called "Natural Forest Areas" will be used as a surrogate for old forests as a means of retaining important attributes for biodiversity conservation while considering operational reality. The intention is to allow a representative quantity of Natural Forest Area to fulfill the old forest retention requirement (BC Provincial Government, 2005). When considering Natural Forest Areas, the following combination of factors can be used as selection criteria:

1) Remnant stands (patches) of live old trees.

2) Partly killed stands (patches) that still maintain the attributes of old forest.

3) Mountain pine beetle killed stands (patches) containing snag attributes.

The Order also states that once there is new information available to verify landscape condition and the extent of mountain pine beetle impact is fully realized, the interim measure for Natural Forest Areas, to ensure species representation will be revisited (BC Provincial Government, 2005).

Also under the order; a licensee affected by an epidemic or catastrophic event may ensure a representative portion of the stand is used to contribute to 'Old Forest' retention and 'Old Interior Forest' objectives by providing a minimum retention for non-pine leading forests for old forest retention in the Moist Interior NDU to encourage some live old forest to be present on the landscape once the current Mountain Pine Beetle epidemic has run its course (BC Provincial Government, 2005).

One of the key objectives of the Chief Forester's "Guidance on Landscape and Stand Level Retention" regarding the retention of Douglas-fir under large scale mountain pine beetle salvage harvesting is to identify landscape and stand level forest retention requirements around existing and naturally occurring retention areas regarding biodiversity levels and the range of natural variability within geographic areas (BC Ministry of Forests, 2005). It is acknowledged under this "guidance document" that spatial distribution is important and that a selection of unharvested stands should include

a matrix of stand ages and species mixes and that retention should focus on older stand types. . Furthermore, spatial definition for retention strategies should consider ungulate ranges and large leave and cut areas with appropriate in-block retention (BC Ministry of Forests, 2005). More specifically, it is stated that where there are Douglas-fir, and other non-pine windfirm trees of good form, reasonable efforts should be undertaken to retain significant portions of that species at the landscape and cutblock level (BC Ministry of Forests, 2005).

In 2002 the provincial government outlined key management issues in the context of "Protecting forest and environmental values". A number of these issues are of concern in areas of the interior where Douglas-fir is at the extent of its northern limits in North America, and plays a significant role in contributing to habitat quality (BC Provincial Government, 2002). Identified as important elements of this policy are the management of critical ungulate winter range (CUWR), wildlife trees, course woody debris, silviculture activities that acknowledge non-timber resource values and landscape level biodiversity (BC Provincial Government, 2002). Part of the rational for retaining these large old Douglas-fir trees at their northern extent, is because of their habitat value (Whittaker, 1996). Apart from the wildlife features created from large dead standing or downed Douglas-fir, live trees that survive wildfire and persist through ensuing younger stands provide mule deer (*Odocoileus hemionus* [Rafinesque]), with critical winter habitat. Winter can be a critical period for mule deer, and Douglas-fir trees in north central British Columbia provide extensive canopy closure in critical ungulate winter range (CUWR) (Whittaker, 1996). Thus, based on regional variance of ungulate habitat

requirements and the identified forest structural criteria (e.g. vertical structure and age class) needed to meet these requirements, Douglas-fir as a species clearly meets forest cover conservation requirements. On a landscape where much of the Douglas-fir present exists as secondary and tertiary stand components, often in smaller clumps associated with optimal site conditions and compensating site factors at harsher environmental extremes (DeLong, 1999), and grows to greater sizes than the other conifer species, its very presence is unique. Its snag recruitment potential as a valuable wildlife tree and its contribution to wildlife habitat associated with course woody debris is in a large part a consequence of its large bole size typical of natural forest conditions in which it is found in Central BC Its importance as a non-timber resource, already identified under land use objectives for CUWR (Brade, 2003 and Vinnedge 2004), requires that we monitor silviculture and harvesting activities and declare sensitive areas associated with Douglas-fir stand components.

4.0 Douglas-fir leave tree mortality: A pilot study

4.1 Introduction

Mortality of Douglas-fir leave-trees in central British Columbia has been widely observed anecdotally but there has been little if any previous systematic examination of this phenomenon. In the spring of 2002, I undertook reconnaissance to select cutblocks with Douglas-fir retention for a pilot study to investigate possible causes in the Prince George and Ft. St. James Forest Districts. Because Douglas-fir has a low tolerance to high water tables (Klinka et al. 2000) and soil moisture content of new cutblocks is known to be greater than that of the adjacent uncut shaded forest (Grifiths and Swanson. 2000) the initial working hypothesis included potential causal factors such as: 1) slope position; 2) moisture regime; and 3) soil texture. It was hypothesized that lower slopes may accumulate more water than normal after harvest putting Douglas-fir leave-trees at this slope position at greater risk than those at higher slope positions. Determining whether this and/or other site factors such as soil texture (drainage capacity) were related to mortality and determining how variable mortality was throughout the study areas was the focus of the pilot study. Percent mortality in relation to slope position and soil texture was subsequently sampled on 12 cutblocks in the SBSdw3 and mk1 BEC subzones during the summer of 2002. This pilot study had two objectives: 1) to determine if any obvious trends existed between mortality and the above ecological site factors and 2) to document spatial variation in levels of mortality by geography and/or subzones.

4.2 Methods

Potential study cutblocks in the SBSdw3 BEC subzone variants of the Prince George and Ft. St. James Forest Districts were subjectively identified through suggestion by industrial collaborators and chosen from forest development plan maps. Study area selection criteria for sites were cutblocks including: 1) scattered retention trees of the size ($\geq$ 30 cm dbh) typically left by the harvesting operators, 2) presence of adjacent unharvested forest must contain enough Douglas-fir representing the same size distribution as those in the cutblock, 3) trees in the unharvested forest must be under the influence of the same site characteristics (e.g. aspect, distribution on slope, soil characteristics). However, finding sites that met the criteria for unharvested forest control proved difficult. Therefore, unharvested areas were only available for 6 of the 12 sites.

4.2.1 Data collection

Stand sampling and initial data collection took place from June 2002 to October 2002 and was carried out in the following manner:

1:5000 scale maps of selected cutblocks were overlain with a 50m x 50m grid. Numbers of plots representing 5 % of the cutblock area were chosen randomly from points on the grid to sample the cutblock and the adjacent unharvested, control stand. Variables collected for live and dead trees are listed in Table 4.1. The initial sampling approach involved sampling with lower intensity and covering more sites rather than intensive

sampling on a few sites. The initial sampling intensity was 20 % but was lowered to 5 % so more sites could be sampled. Twelve sites in total were sampled.

4.3 Results and discussion

Trends in leave-tree mortality were examined by site, subzone, slope position, and soil texture. Mortality data was also pooled in order to examine any trends that may be common across all sites. It is evident from DeLong (1999) that Douglas-fir establishment in colder, wetter subzones is related more closely to aspect and percent slope than in warmer dryer subzones. Thus, there was an interest in determining whether postharvest leave-tree mortality may follow the same pattern.

Because this was an exploratory pilot study, sample intensity among sites was unbalanced, as we attempted to refine sampling methods that were limited by the availability of appropriate operational prescriptions, and by field logistics. Availability of control areas was limited and sometimes absent given logging practices. Only descriptive statistical analysis was conducted on this data due to the above limitations.

Generally mortality was greater in cutblocks on the logged sites and low or absent on adjacent unharvested areas when sampling occurred on them (Figures 4.1 and 4.2). Average percent mortality in cutblocks pooled by geographic area or BEC subzone seen in Table 4.2 indicated higher mortality in the SBSdw3 (dry) subzone (23.2, sem $\pm$ 8.7) in comparison to the SBSmk1 (moist) (16.0, sem $\pm$ 10.0) subzone. However, the standard

error of the means suggest that the two subzones are not significantly different ($\alpha = 0.05$). The high degree of variability among cutblocks for mortality was one of the primary difficulties that prevented further statistical comparisons without having much larger sample sizes. Total stems, live and dead stems for harvested and unharvested units and average cutblock mortality for the pooled data is also presented in Table 4.2. Data pooled from all study plots for all sites showed no clear pattern (Figures 4.3 and 4.4) to suggest that mortality varies along gradients of soil texture and slope position. Most trees were found on coarse textured soils with a higher sand content. Most of the trees on loam soils died but the sample size was small.

Assessments of percent mortality data indicated that mortality was spatially highly variable. Although it was hoped that in this phase of sampling, data suitable for examining correlations between mortality and the above mentioned variables would be collected, this was not the case. With the large number of cutblocks that would be necessary to meet statistical confidence limits, given available resources, this approach was no longer an option. Constraints such as unattainable sample sizes to overcome in-block spatial variability, variable stand conditions and leave-tree dispersal characteristics and difficulty locating appropriate random plots in adjacent unharvested areas limited the opportunity for statistical comparison between treatments and cutblocks. However, this phase of the investigation did provide critical baseline information addressing a broad range of site and harvesting characteristics in relation to leave-tree mortality.

The only trend seen in the data was the low mortality in the unharvested versus the harvested treatments. This suggests that the leave-tree mortality may be happening at a much greater rate than mortality in the unharvested stand.

It was evident from the highly variable nature of leave-tree dispersal and density on the cutblocks, that in order to meet statistically sound sample size requirements for parametric analysis, the number of plots needed far exceeded our resources. Results were also confounded by the spatial nature of leave-tree distribution throughout the cutblocks as a result of decisions made by the harvesting operator and/or block layout crew and the effect that this has on sampling error. For example, in many cases cut block boundaries ended before the slope crest. Therefore, the low number of trees seen in the crest class is a result of where cutblock boundaries were established and has no ecological bearing. It is however, evident from this data that Douglas-fir retention is most abundant on mid to upper slope positions where they naturally proliferate. These factors contributed to a large sampling error in the initial sampling design that could only be overcome with much replication while some blocks such as those with block designs that introduced bias could not be. However, in conjunction with field observations, these data sufficiently describe the variable nature leave-tree dieback levels occurring in the SBS. Natural mortality for trees in the unharvested stands is much lower than that of leave-trees in the cutblock. Interestingly site 7 had mortality in the control but not on the logged area. Evidence of previous bark beetle attack was observed in the area of this site, and may explain this, as trees killed by bark beetle in the cutblock would have been felled by the harvesting operators.

There were no clear patterns for the mortality of Douglas-fir leave-trees in relation to site factors. Moreover, levels of mortality seen across soil texture and slope position classes are more likely a reflection of higher Douglas-fir abundance on portions of sites that were optimal in relation to Douglas-fir silvics and ecological amplitude (Herman and Lavender, 1988). Mortality in unharvested stands occurs at a much lower rate than that of the harvested stands.

However, the actual mortality rate of Douglas-fir leave-trees after fire disturbance, the primary influence on their distribution on the landscape (BC Ministry of Forests, 1995), is not known. To more accurately predict what natural mortality rates have historically been, a retrospective investigation into remnant evidence of dead Douglas-fir trees in stands with known fire histories could to be undertaken.

It became evident, after analysis of the data from this pilot study that there may be numerous factors for any given tree that contribute to its mortality (Table 1.1). The establishment of sampling units appropriate for statistical analysis of Douglas-fir leave-tree mortality on cutblocks with variable features and sizes proved to be difficult with the initial study design. Determining the cutblock and unharvested areas to be sampled provided the greatest challenge due to high spatial variability in retention dispersal characteristics which would have resulted in high standard error given the we did not have the resources to obtain needed sample sizes. However, information gathered from sampling in 2002 provided a foundation for further investigation.

Observations of crown characteristics consistent with drought were observed on many Douglas-fir leave-trees on cutblocks ranging from 1-8 years since logging. This appeared contrary to current literature which suggested available soil moisture would be higher in the cutblocks than in the adjacent, unlogged controls, thus a question of why drought symptoms were being observed arose. The observations of drought symptoms and the hypotheses that single leave-trees retained in cutblocks would be under greater water stress than trees in adjacent harvest areas provided direction for the sampling approach to measure water relations around individual trees in unlogged and harvested treatments in 2003.

Occasionally in cutblocks with Douglas-fir single tree retention, bark beetle was observed in dead and dying trees. However, this was infrequent and it was believed that the beetle was present as a secondary agent. Extensive observation of Douglas-fir leave-trees over the 2002 growing season revealed no obvious pathogens or damage agents associated with dead or low vigour trees. Some physical scarring of tree boles and lateral roots from harvesting operators was evident but minimal.

It was decided that a) focusing on one parameter and either accepting or rejecting that hypothesis should be the object of this research and b) it would be better to definitively rule out or accept one quantitative factor than to attempt meeting larger sample size requirements of the initial design and approach. The proposed methodology would be the first step in a reductionist approach to defining potential agents for Douglas-fir leave-tree mortality. Thus, the new study approach was based on the empirical factor of water

relations: how this differs between Douglas-fir leave-trees in harvested versus unharvested units.

4.0 Tables and Figures:

Table 4.1. Variables collected for live and dead Douglas-fir trees in each grid plot in 2002

Data
-DBH
-total height
-crown condition
-% live crown
-vigor
-pathological indicators
-logging and natural damage to bole and/or lateral roots
-tree cores at breast height
-soil texture
-rooting restriction
-slope position
-% slope
-aspect
-wildlife habitat attributes

Table 4.2. Total stems, live and dead stems for harvested (cc) and unharvested (un) units and average cutblock mortality for sites pooled by dry and moist ecosystem.

Precipitation	Total stems (cc)	Total stems (un)	# Live stems (cc)	# Dead stems (cc)	# Live stems (un)	# Dead stems (un)	Pooled average % mortality (cc)	SEM
Dry (dw3)	131	173	110	21	168	5	23.2	8.8
Moist (mk1)	35	64	31	4	63	1	16.0	10.0

Figure 4.1. Percent mortality detected in cutblocks at each site. Sample size (n) at each site was: 1 = 22, 2 = 20, 3 = 2, 4 = 5, 6 = 2, 7 = 27, 8 = 12, 9 = 7, 10 = 3, 11 = 2, 12 = 36.

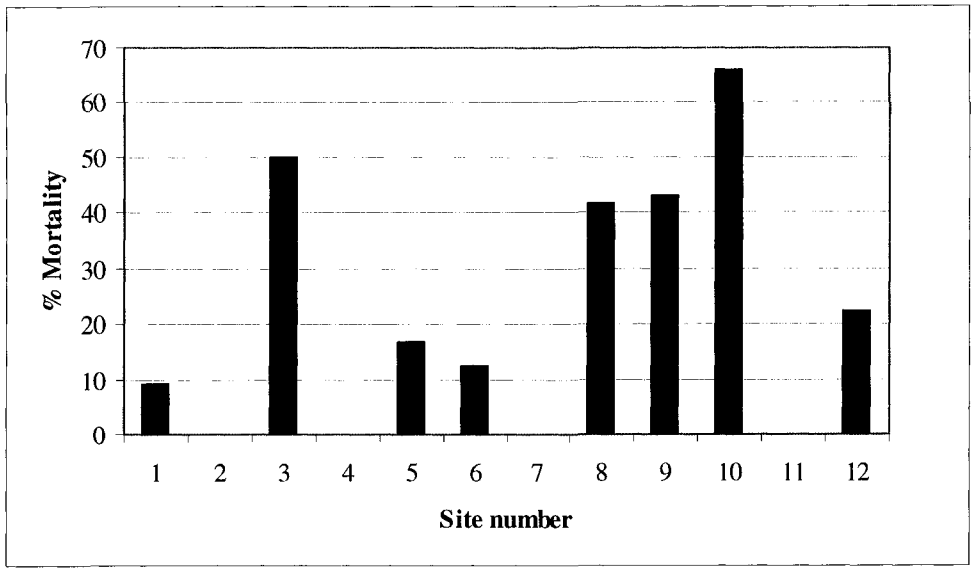


Figure 4.2. Percent mortality in unharvested areas at each site, plots were sampled in adjacent unharvested areas. Sample size (n) at each site was: 3 = 51, 5 = 13, 6 = 60, 7 = 32, 8 = 81.

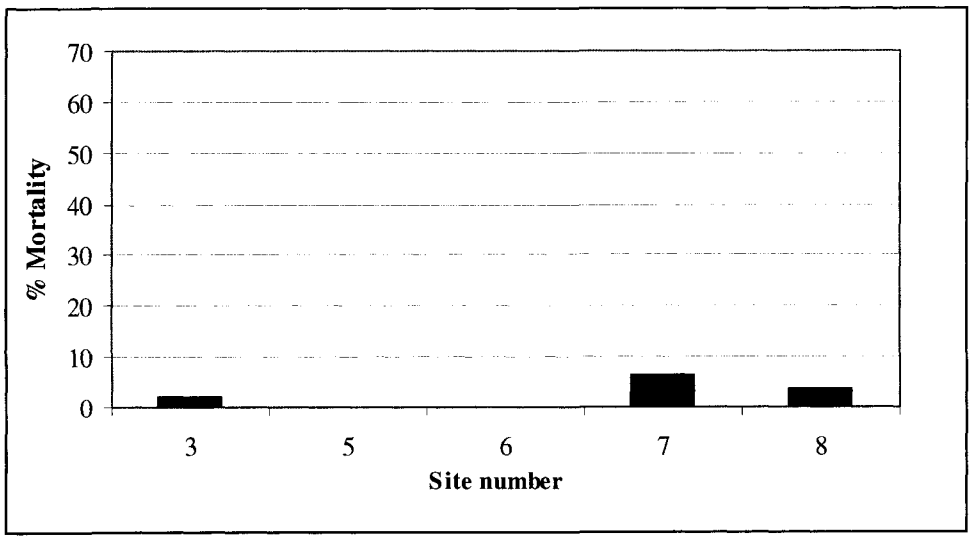


Figure 4.3. Percent morality by soil texture class for all clearcut plots.

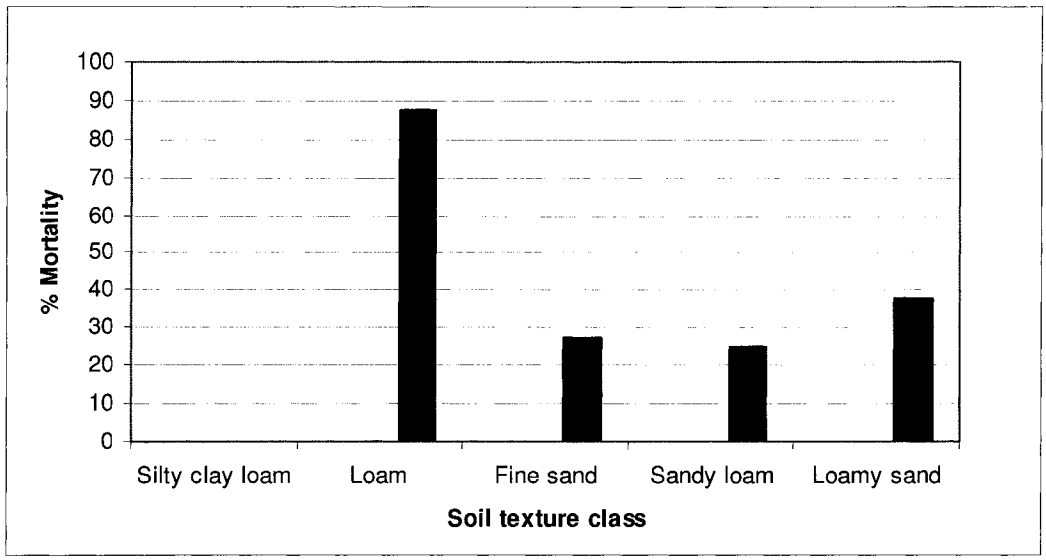
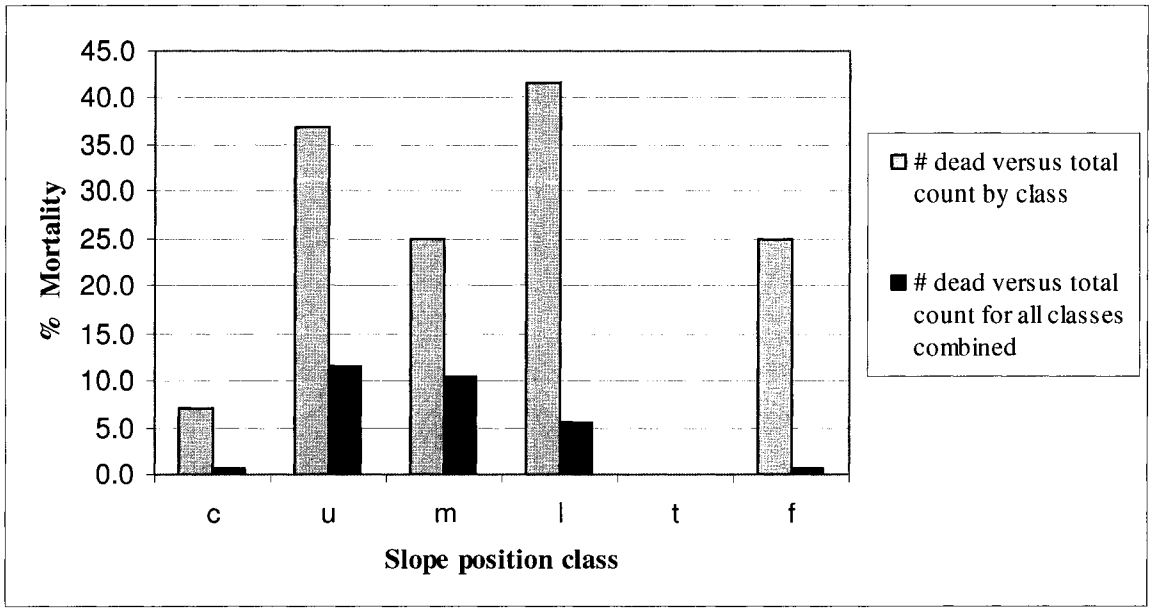


Figure 4.4. Percent mortality by slope position for the number of live and dead trees detected in each slope position class (Total count by class) (c=crest, u=upper, m=mid, l=lower t=toe and f=flat), and % mortality by slope position for the number of live and dead trees detected from all slope position classes combined (Total count all trees combined).



5.0 Plant and soil water relations: 1) Water potential

5.1 Introduction

In June of 2003 a study to examine possible differences between xylem water potential between single Douglas-fir leave-trees on cutblocks and their equivalent cohorts in adjacent unharvested forest commenced to determine if observed leave-tree mortality was related to water stress. The working hypothesis of the study was that the trees in the harvested units would attain higher levels of stress more frequently throughout the growing season.

Plant moisture stress or tension created within the tree results from inadequate water uptake between the roots and the surrounding soil environment. It can be measured to determine a plant's response to water availability (Wilson, 1984). The stomatal response of leaves has been shown to be more sensitive to VPD, than to photosynthetically active radiation (PAR) (Fischer et al. 2002). This tension results from leaf transpiration processes and the plant's failure to acquire water quickly enough to balance the water loss from the leaves (Waring et al. 1967). Commonly, measured water stress can be higher during the day than at night due to diurnal changes in stomatal response (Burns et al, 2003).

Waring and Cleary (1967), describe the technique for measuring twig water potential (ψ_T) which was the primary variable in this study. It is a well established and accepted method

that has seen wide application since the early 1960's with the use of a pressure chamber or pressure bomb (PMS Instrument®, Corvallis, OR) (Waring, et al. 1967, Kaufman, 1968, Duniway, 1971, Cleary and Zaerr, 1980, Sperry and Ikeda, 1997, Bond and Kavanagh, 1999, Stout and Sala, 2003, Woodruff, et al. 2004).

The level of transpiration taking place at the tree level is of interest when considering water input and output as it cycles from the ground, through the tree, and into the atmosphere. Temperature plays an important role in this process. The temperature of the aerial parts of plants is determined by the balance between energy gain by interception of radiation and the energy losses by the re-radiation, convection or sensible heat loss and transpiration (Coombs, 1985). The water content of air is known as the absolute humidity and is the density of water vapor in the air. The importance of humidity to the plant is two fold. First it determines the rate of water loss in transpiration, and second it has a direct effect on the stomata of many plants such that stomata tend to close in dry air restricting water loss but also reducing CO_2 assimilation (Coombs, 1985). Depending on the species, and the severity of the water stress, large reductions in photosynthesis over time can reduce tree vigor and may actually be from leaf area reductions, due to leaf shedding, or by the delay of leaf growth and development (Jones 1992). Relative humidity is the ratio of the actual vapor pressure to the saturated vapor pressure at dry bulb temperature. However, plants do not respond directly to relative humidity. Saturation deficit, or vapor pressure deficit is the difference between the saturation vapor pressure and the actual vapor pressure at the same temperature. It is an index of the

drying power of the air; the higher the deficit the greater the evaporation rate or demand (Coombs, 1985).

Predawn measurement of plant water potential reveals the water potential of the tree when at approximate equilibrium with the soil while stomata are open and respiration is taking place. Disequilibrium between soil water potential and predawn water potential can indicate insufficient recharge of stem water storage (Bucci et al. 2004). Predawn leaf water potential and xylem pressure potential are often used as surrogates for soil water potential based on the expectation that predawn plant water potential is in equilibrium with the wettest soil water potential accessed by the roots (Ritchie and Hinckley, 1975, Hinckley et al. 1978 and Richter, 1997). Classical water relations theory predicts that predawn plant water potential should be in equilibrium with soil water potential around roots, and many interpretations of plant water status in natural populations are based on this expectation (Donovan et al. 1999). However, numerous other mechanisms can also be responsible for predawn 'disequilibra' between plant and soil water potential (Donovan et al. 1999).

One possible mechanism postulated that predawn water potential disequilibria (predawn plant water potential was more negative than soil water potential) observed in tropical savanna woody species was insufficient time for the recharge of cell water storage compartments (Bucci et al. 2004). Pathogens on Douglas-fir such as dwarf mistletoe (*Arceuthobium*) also limit the supply of water to the leaves, especially under high evaporative demand, resulting in significantly more negative (greater stress) predawn leaf

water potentials in comparison to uninfected trees (Sala et al. 2001). Although the mode behind available water limitation leading to diminished recovery and recharge in Sala et al. (2001) may differ from that of Douglas-fir leave-trees, the ultimate result, insufficient nocturnal water recharge is the same.

Other than general relationships, little is known about the sensitivity of Douglas-fir leave-trees to changes in local hydrology and micro environment. If pre and postharvest changes in water relations (e.g. soil moisture and water availability, atmospheric demand for water) occur around Douglas-fir leave-trees, it should be reflected in its physiological response to varying levels of water stress.

The objectives of this study were to determine whether: 1) sampled Douglas-fir leave-trees in clearcut (cc) treatments are subjected to greater stress more frequently throughout the growing season than nearby trees of the same cohort in unharvested (un) treatments, and 2) stress levels differ between a recently harvested (0-year) leave-tree site and one harvested 5-years prior to sampling (5-year).

5.2 Methods

5.2.1 Site and sample tree selection

5.2.1.1 Site selection

At the northern extent of its range in British Columbia, interior Douglas-fir occurs primarily on warmer aspects and in drier subzones (DeLong, 1999). Therefore primary sampling took place in SBSdw3/dw2 (dry, warm) subzone because stands in this ecosystem have a greater Douglas-fir component than stands in other SBS subzones.

Two sites were chosen in the SBSdw3 subzone approximately 40 km south of Prince George British Columbia (Figure 5.1). They are representative of many stands with Douglas-fir components at this latitude, consisting of 3 age cohorts (approximately 120-years, 200+ years and 300+ years) of Douglas-fir mixed predominantly with lodgepole pine (*Pinus contorta*) and interior hybrid spruce (*Picea glauca x P. engelmannii*). Based on the similar age distribution of Douglas-fir cohorts and evidence of previous fires at both sites, it is assumed that they have similar disturbance histories. Each site was winter harvested, one the previous winter (0-year site) and the other 5-years earlier (5-year site).

All site selection criteria where designed to minimize site and ecological variation within and between sites. For both sites criteria for site selection were as follows: 1) location in the SBSdw subzone variant with similar climatic influence, 2) similar edaphic conditions

(mesic to subhygric with poor to moderate nutrients), 3) surface shape is flat to gently rolling with no immediate hydric relief, 4) similar fire disturbance history (both sites had older fire veteran trees amongst younger cohorts), 5) same seral stage/successional status (both sites are mature seral stage), and 6) both sites were harvested in winter. Each of the listed criteria for site selection were chosen for the following reasons: 1) micro and mesoclimates directly influence plant water relations, 2) edatope represents moisture regime and hence available water, 3) surface shape influences drainage characteristics and hence available water 4) and 5) distribution of age cohorts/seral stage influence typical leave-tree age class distribution and thus tree vigor, and 6) season of harvest influences soil postharvest soil properties and/or direct lateral root damage and thus available water. Along with these parameters, % vegetation cover was also measured around the sample trees. Inter-tree spacing within a treatment, health status, size, and distance to trees in adjacent treatments were considered to minimize impacts that spatial site variability might have on individual tree water relations. Two representative sites were selected. Within each site a control treatment area was situated adjacent to the clearcut treatment area.

5.2.1.2 Sample tree selection

Criteria for sample tree selection were as follows: 1) size (diameters and heights) representative of the range chosen by harvesting operators, 2) no obvious pathological or damage agents, and 3) sample trees in treatment areas within 30 m of each other with

similar site characteristics. Sample tree descriptions for the un and cc treatments at the 0-year and 5-year sites are shown in Table 5.1.

Two trees per harvested and unharvested treatment were selected in close proximity to each other (10-30 m). Initially, groups of single retention trees were located within each treatment. Two trees were selected by walking into the group and picking the first closest tree (Tree 1) that met the selection criteria. Tree 2 was the closest tree to tree 1 that met selection criteria. Each tree was then assessed to ensure it had no apparent damage or health concerns. Additionally, two trees that exhibited apparent characteristics of water stress were also deliberately selected at the 5-year site in the cc treatment for occasional sampling. The first (Tree 3) had top dieback and the second (Tree 4) exhibited crown thinning.

5.2.2 Water potential data collection

Evaluation of water relations was achieved by: 1) examining the frequency at which midday and predawn twig water potential values fall within low, moderate and high stress categories in cc versus un treatments, 2) determining whether differences in microsite environment such as VPD, soil moisture and temperature and wind speed exist between cc and un treatments and, 3) determining whether patterns seen in the 0-year site differed from that of the 5-year site.

Twigs were sampled from within the top 5 meters of each sample tree using a 12 gauge shot gun with No. 2 lead shot Winchester® 2 ¾ inch heavy game load rounds. Twig water potential (terminal shoot moisture status) was then measured immediately on site with a pressure chamber (PMS Instrument®, Corvallis, OR). Midday measurements were taken weekly and initially, predawn measurements were taken biweekly. However, after predawn trends were determined the frequency of these measurements was reduced. Midday measurements were taken between 1130 hours and 1400 hours (PDT) revealing twig – leaf water potential at the time of maximum midday water demand and probable stomatal closure (Bond and Kavanaugh, 1999). Predawn measurements were taken anywhere from 0100 hours to 0400 hours. Dawn occurs at about 0400 hours from early June to mid July (Environment Canada, 2006)[3].

Three random twig samples were collected and measured from each tree at each sample time. Teflon tape was wound around the twigs before they were inserted into the rubber stopper in the pressure bomb to ensure that there was no air leakage when pressure was applied. Shooting heights for twig removal varied from tree to tree due to tree height, crown shape and visual accessibility. Therefore heights for each sample tree at both sites were established using a Laser Hypsometer ® and field measurements of plant moisture status were corrected for gravitational height effects during data summary. Because final analysis required comparisons of all trees in all treatments across both sites, all trees were standardized to the lowest shooting height. As tree height increases, water potential falls by 1 Bar or 0.1 MPa for every 10 m change in height (Bauerle et al. 1999, Spicer and

[3] Environment Canada. (Updated July 8, 2006) Canadian Weather Center, Prince George. http://www.canadiancontent.net/weather/bc/prince%20george/

Gartner, 2001, Meinzer, 2003 and Woodruff et al. 2004). Thus, because water potential values within and among sites were to be compared, the differences in twig removal height between all trees and the tree with the lowest twig removal height (standard twig removal height of 26.6 m) were established using a gravitational height correction calculation. The 'gravitational height correction value (MPa)' seen in Table 5.2 was subtracted from the individual twig water potential values for every sample.

5.2.3 Water potential data analysis

Experimental units were treatments (cc and un) and sites (0-year and 5-year); sample units were trees (2 per treatment) and measurement units were individual twigs (e.g. 3 twigs per sample tree per day).

Histograms with normal smoothing curves representing seasonal twig water potential values for combined trees in each treatment were generated in SYSTAT® v. II for each study site in order to visually assess data distribution.

Two-sample *t*-Tests Assuming Unequal Variances with a null hypothesis of equal proportions ($\alpha = 0.05$) (Wackerly et al. 2002) were used to determine whether there were significant differences in seasonal water potential values for trees within the cc and un treatments under midday and predawn conditions at the 0-year and 5-year sites and whether values from each tree within treatments could be combined for further analysis.

For combined trees in each treatment all individual twig water potential values throughout the sampling season were placed into three twig water potential stress categories (low, moderate and high stress); i) $\geq$ -1.6 KPa, a range representing values higher (more positive/less stress) than that generally considered to be the soil water potential at which permanent wilting point occurs in plants (Van der Ploeg et al. 2005). If soil water is held at water potentials more negative than -1.5 MPa it is generally considered to be unavailable to plants (Salibury and Ross, 1978, Raven and Ross, 1992); ii) < -1.6 MPa and > -2.9 MPa representing a normal functional range for Douglas-fir. Douglas-fir achieves a threshold leaf water potential at approximately -2.5 MPa, where stomatal closure takes place to minimize transpirational water loss (Bauerle et al. 1999 and Bond et al. 1999 and); and iii) $\leq$ -2.9 MPa representing a range of water stress where physiological damage may occur in the trees. A leaf water potential value of -2.9 MPa was selected as the cutoff point for the 'high stress' categories to ensure that twig sample values where substantially more negative than the -2.5 MPa lower limit of the 'normal' category threshold. Prolonged exposure of Douglas-fir to leaf water potentials exceeding -2.8 MPa can be physiologically damaging to the tree (Bond, 2003)[4].

Using the method outlined above, data were analyzed in three ways: i) all twig values combined for the sample season by treatment within sites, ii) twig values were split into 'high' versus 'low' VPD groupings independent of date by treatment within sites to examine differences in water potential stress categories between treatments. The range of

[4] Bond, Barbara J., 2003. (Personnel Communication) Professor, College of Forestry, Department of Forest Science, Oregon State University 321 Richardson Hall Oregon State University Corvallis, OR 97331

values for each of the high and low VPD groups was split using 1.2 MPa as it was the midpoint value for both sites, and iii) all values combined for the sample season were compared among sites for differences between water potential stress categories. To compare two proportions, the hypothesis under test were H_o: $P_1 - P_2 = 0$ versus H_a: $P_1 - P_2 \neq 0$, and the z-statistic was used where P is an observed proportion (Johnson, 1992).

An example of how proportional statistics were calculated for seasonal values is presented in Table 5.3. In steps $\mathbf{A_1}$ and $\mathbf{A_2}$ (cc and un treatments respectively) in rows for trees 1 and 2 are the values for total number of twig sample measurements that fell into the low, moderate and high stress categories. Column totals indicate the observed frequencies of twig values for both trees combined that occurred in each water potential stress category (x1) and for all categories combined (n1) over the sampling season. Row totals indicate the observed frequencies twig values for trees 1 and 2 from all categories combined over the sampling season. These values were then used to calculate the observed proportions (p') seen in step **B**. Pooled observed proportions (P'_p) and z-statistics seen in step **C** and **D** respectively were then calculated for each water potential stress category using equations 1 and 2 (Johnson, 1992):

1) $\boldsymbol{P'_p} = (x1+x2)/(n1+n2)$ and $q'_p = 1 - P'_p$

2) $z = P'_1 - P'_2/\mathrm{SQRT}((P'_p * q'_p[(1/n1)+(1/n2)])$

Where the observed pooled probability is $P'p$, x is the number of success in n trials, p is the probability of success in an individual trial and q is the probability of failure in each trial.

A table of p-values for Standard Normal Distribution was then used to determine if differences for the frequency of the combined tree values in each category seen between the un and cc treatments within each site were statistically significant ($\alpha = 0.05$) (Wackerly et al. 2002).

Mean midday and predawn seasonal values with standard error and confidence intervals were also calculated for each tree at each site. Sample sizes within and among trees and treatments were dictated by how many individual twig samples were taken for each tree from the beginning to the end of the sample season or other defined time interval.

Regression analysis was then performed in Microsoft Excel® 2002 to examine the relationship between twig water potential values and increasing VPD. This was carried out independent of which month the values occurred, with VPD values sorted in increasing order with the corresponding twig water potential values from the same sample day using the previously described VPD grouping.

Seasonal cumulative twig water potential values were calculated for each tree to observe relative water stress loading. Most trees are exposed to some degree of water stress, but it is the duration of stress that is more relevant to injury or mortality (Decoteau, 2005).

Greater exposure over the growing season to more demanding water conditions as a result of increased VPD and/or insufficient available soil water in relation to atmospheric demand, can stress trees beyond the point of physiological recovery (Jones 1992, Kozlowski and Pallardy 1997, Bond et al. 1999, Simpson, 2000, Decoteau, 2005). To determine stress loading on individual trees, cumulative water potential values for each tree were calculated by simply summing the individual twig values for each tree progressively, by sample days throughout the growing season for comparison. Only data from sample days where each tree was sampled (2 trees in the cc and 2 trees in the un treatments) for 3 twig values per tree were used in order to maintain values that were balanced for same number of samples taken on the same days. Because water potential ranges for individual trees can vary day to day with weather conditions, this approach ensured that not only were sample sizes equal, but that the values summed were all functions of the same environmental conditions. Equipment failures and weather conditions sometimes resulted in deficient twig numbers or missing trees on certain sample days which were ultimately excluded from calculated sums. Because the number of usable sample days (e.g. those with equal sampling effort occurring on the same day) varied between sites, the cumulative water potential values are a reflection of individual site predawn or midday sampling effort and unique to available sample days at each site. Therefore, in many cases, sites were sampled on different days with different weather conditions I had different usable numbers of samples and between-site comparisons of these values could not be made.

5.2.4 Atmospheric transpirational demand

To measure 'local area' atmospheric demand or VPD in 2003 for the sample trees, mean hourly temperature and relative humidity data for the 2003 growing season from two local area fire-weather stations (within 10 km of each site) were used to calculate VPD. The weather stations used Forest Technology Systems Ltd. (F.T.R) temperature/relative humidity sensors (Model THS-62). The following empirical equations (equations 3, 4 and 5) were use to calculate VPD (Jackson, 2004 Pers. Com)[5]:

3) $Es = (6.11 \times 10)^{(7.5 \times Tc/(237.7+Tc))}$

4) $E = RH \times Es$

5) $VPD = Es - E$

where Tc is the temperature in C, RH is the relative humidity, Es is the saturation vapor pressure, E is the calculated vapor pressure and VPD is the vapor pressure deficit. Data were converted from hPa and reported in kPa.

For the 2004 growing season, two climate stations were erected at a site in the SBSmk1/dw3 subzone to compare 'site level' VPD in the cc treatment with that of the un treatment. The intent was to observe trends between the treatments that could be used validate assumptions of differences in VPD between treatments in the 2003 data. In each treatment unit at least 100 m from forest edge, Vaisala temperature/relative humidity sensors (Model HMP 35A) were mounted 10 feet above the ground on aerial towers and

[5] Jackson, Peter, 2004. Personal communication. Associate Professor Environmental Science & Environmental Engineering Programs, College of Science and Management, University of Northern British Columbia, Prince George, British Columbia.

fitted with PVC radiation shields. The above empirical equations (3, 4 and 5) were programmed into the data logger with the output data in kPa units.

To measure daily wind speed, cup anemometers were fastened 10 feet above the ground in the cc treatment of the 0-year site and both the cc and un treatments for the 5-year site. Data were compiled in Campbell Scientific® CR10X data loggers as hourly averages.

5.3 Results

5.3.1 Seasonal water potential

Twig water potential data distributions for combined trees at the 0-year and 5-year sites cc and un treatments all approach normal distribution (Figure 5.2).

For *t*-Tests at the 0-year site the cc and un midday and predawn p-values are not different and the data can be pooled for further analysis (Table 5.4).

At the 5-year site, trees 1 and tree 2 in the cc treatment are not significantly different (p = 0.0659) and can be pooled for further analysis (Table 5.5). Trees 1 and 2 from the un midday and cc and un predawn treatments are significantly different. Thus, pooling data for these 2 trees may violate statistical assumptions (Table 5.5).

When the frequency of occurrence of twig values for all trees in both cc and un treatments at both sites that fell within the 3 water potential stress categories (low, normal and high) are expressed as percentages of the total number of twigs sampled throughout the season, both trees in the cc treatment of the 0-year site have twig values occurring more frequently in the high stress category than those in the un treatment (Figure 5.3). For the un treatment, most values occurred in the normal category and a few in the low category. This was not true for the 5-year site which had very few values that fell within the high stress category in either of the treatments. For the cc treatment of the 5-year site, a greater percentage of values occurred in the low stress category compared to the un treatment which had more values occurring throughout the season in the normal category (Figure 5.3).

The observed proportional differences for the high stress categories between un and cc treatments in the 0-year site were significant ($p = 0.0002$), while that of the 5-year site were not ($p = 0.4207$) (Table 5.6). Each month throughout the season, the most negative mean water potential values occurred in the cc treatment of the 0-year site, while the opposite was true for the 5 year site, with the most negative mean values occurring in the un treatment (Table 5.7). The 0-year site cc treatment had the most negative monthly mean values of all treatments in all sites (Table 5.7). Standard error was generally high for these means due to small samples, when examined monthly.

When proportional differences for water potential categories between un and cc treatments were analyzed by 'Low' versus 'High' VPD grouping independent of month

(Low = ≤ 1.20 KPa and High = > 1.2 KPa), no significant differences were seen between cc and un treatments in the Low VPD grouping for the 0-year site (Table 5.8). However in the High VPD grouping the 'normal stress' and 'high stress' water potential categories were significantly different (p=0.0002 for each) with 84% of the twig values for the 'normal stress' category seen in the un treatment versus 43% in the cc treatment and 57% for the 'high stress' category seen in the cc treatment versus 16% in the un treatment. The only significant difference seen between treatments for the 5-year site was in the 'low stress' water potential category where 32% of the cc values and 9 % of the un values (p= 0.0122) fell into this category (Table 5.9).

When the 0-year and 5-year sites were compared seasonally by cc and un treatment for proportional differences in frequency of occurrence for values in twig water potential (wp) stress categories, the 5-year site had significantly more values in the 'low stress' and 'normal stress' categories. However in the 'high stress' category, there were significantly more values observed at the 0-year site (Table 5.10).

Midday twig water potentials averaged across the growing season for each tree were more negative for trees 1 and 2 in the 0-year clearcut cc treatment (Figure 5.4) than in the unharvested un treatment. For the 5-year site, sample trees 1 and 2 in the cc have equal if not 'better' midday seasonal water potential than tree 1 and 2 in the un (Figure 5.4). In the 5-year cc treatment tree 3 with top die-back, had similar mean seasonal midday water potential to that of the trees 1 and 2, while tree 4 was more negative (Figure 5.4). In the 5-year un, tree 1 appears to have lower seasonal water potentials than all of the other

sample trees. Midday and predawn seasonal means with standard error and confidence intervals for individual trees in all treatments can be seen in Table 5.11.

Predawn water potentials for tree 2 in the 0-year cc were more negative than those for tree 1 and 2 in the un, which were less negative than all other treatment trees across both sites both sites (Figure 5.5). Seasonal predawn water potentials for tree 1 in the 5-year un were more negative than that of all other treatment trees across both sites (Figure 5.5). Midday and predawn daily means with standard error for individual trees in cc and un treatments at both sites can be seen.

Regression statistics for increasing independent variable VPD, plotted against increasing (becoming more negative) dependent variable twig water potential independent of date for the cc and un treatments at the 0-year and 5-year sites can be seen in Figure 5.6.

5.3.2 Daily water potential

Figures 5.7 – 5.10 show daily midday and predawn means for sample trees throughout the growing season for 0 and 5-year sites. Early in the season most trees at the 0-year site (Figure 5.7) show more positive water potentials and are similar to each other except for tree 2 in the cc. During midsummer however, trees in the cc generally have lower water potentials than those in the un, reaching values exceeding -3.50 MPa. Toward the end of summer and into fall, most trees again have minimal differences between them and appear to be recovering more frequently during the evenings. However, tree 2 in the 0-

year cc began and ended the season with very low midday water potential of -4.52 MPa and -3.81 MPa respectively (Figure 5.7).

At the 5-year site, similar over all trends for more positive midday water potential in the spring and fall versus more negative water potentials in midsummer was observed. However, most trees did not fall below (-2.80 MPa) in either cc or un treatments as was seen in the 0-year site (Figures 5.7 and 5.8). During the early spring, tree 4 in the cc (chosen because of low crown vigor) showed a water potential of -4.10 MPa, while in late summer/ early fall sample tree 2 reached a low water potential in relation to the other trees of -3.20 MPa. Figures 5.9 and 5.10 indicate that predawn measurements for each site are similar, but that some trees in the 5-year site have slightly lower predawn water potentials than those of the 0-year site.

In July and August when local area VPD exceeded 1.5 KPa, twig water potential values of -3.02 MPa in the 0-year un treatment to -3.59 MPa in the cc treatment were observed (Table 5.12). However this was not the case at the 5-year site where water potentials associated with VPD above 1.5 KPa did not exceed -2.6 MPa in any treatments (Table 5.13).

Both trees 1 and 2 in the cc treatment at the 0-year site ended the season with higher cumulative daily midday twig water potential values than trees 1 and 2 in the un treatment. This trend was consistent throughout the season (Figure 5.11). Conversely, both trees 1 and 2 in the un treatment ended the season with higher cumulative midday

values than both trees in the cc treatment of the 5-year site (Figure 5.12). For the 0-year site, the trend for both trees in the cc treatment maintaining higher cumulative values throughout the season for predawn measurements was repeated (Figure 5.13). Although at the end of the season the final predawn cumulative value for tree 1 in the un treatment at the 5-year site was the highest, tree 1 in the cc treatment remained the second highest for most of the season (Figure 5.14).

5.3.3 Atmospheric transpirational demand

5.3.3.1 2003 local area vapor pressure deficit and wind speed for 0-year and 5-year sites.

Mean monthly values from daily periods between 1100 and 1300 hours at the 0-year site ranged from 0.88 KPa in May, peaked at 1.41 KPa in July and fell to 0.68 KPa in September (Tables 5.12 & 5.14). For the 5-year site values were 1.25 KPa in May, 1.45 KPa in July and 0.66 KPa in September (Tables 5.13 and 5.15). The seasonal mean and cumulative sum values for the same daily time period were greater at the 0-year site than at the 5-year site

For the 5-year site, average daily wind speed throughout the portion of the sampling season where the anemometer in the un treatment was functional, was higher in the cc treatment compared to that of the un treatment. In the cc treatment the average hourly wind speed was 2.37 m/s (SEM = 0.05) reaching a maximum seasonal value of 3.33 m/s

(early June – late July) while the average for the un treatment was 1.33 m/s (SEM 0.03) reaching a maximum of 1.78 m/s (early June – late July) (Figure 5.15 and Table 5.16).

The anemometer in the cc treatment of the 0-year site was functional from early July until late September maintaining windspeeds higher that that of the cc treatment at the 5-year site throughout the season. In the cc treatment the average wind speed was 2.84 m/s (SEM = 0.05) reaching a maximum seasonal value of 4.62 m/s (early June – Late September) (Figure 5.15 and Table 5.16).

5.3.3.2 2004 site level vapor pressure deficit in cc and un treatments for SBSmk1/dw3 site.

At the end of August 2004 climate stations in cc and un treatments at a site in the SBSdw3/mk1 subzone VPD were down loaded and there were differences in VPD among the treatments (Figure 5.16). Greatest daily maximum values in the un and cc treatments for June, July and August ranged from 2.91 kPa, 2.62 kPa and 2.62 kPa in the un treatment to 4.20 kPa, 4.38 kPa and 4.40 kPa in the cc treatment respectively. Lowest daily maximum values for June, July and August in the un and cc treatments ranged from 0.63 kPa, 0.31 kPa and 0.20 kPa for the un and 0.94 kPa 0.31 kPa and 0.20 kPa for the cc treatments respectively.

5.4 Discussion

Results for midday and predawn twig water potential measurements suggest that hydrological relationships around large Douglas-fir trees under pre and postharvest conditions do vary temporally and spatially in the SBS zone. However, sample sizes for twig water potential measurement units (twigs) ranged between 41 and 55 for sample trees throughout the season, but number of sampling units per treatment (trees) was two. Thus the reader must be cautioned that inference and reliability from these results are limited due to a small sample size.

Douglas-fir leave-trees in the cc treatment at the 0-year site were subjected to greater stress more frequently throughout the growing season than nearby trees in the un treatment, while those of the cc treatment at the 5-year site were not. Most trees endure times of low (negative) water potential and water stress. However, frequently stressed trees are physiologically impacted more than those who undergo sufficiently negative water potentials less frequently (Decoteau, 2005). A deliberately chosen tree that was occasionally sampled at the 5-year site in the cc treatment exhibited visual symptoms of water stress (crown thinning and epinastic leaf curling). It had on average, lower seasonal water potential than the two randomly selected sample trees, while another tree with top die-back that was occasionally sampled showed no signs of water stress. For the tree with top dieback, the live remaining foliage that provided the samples was at the base of the original crown. Thus, the gravitational effect on water potential would be reduced because of the reduced height (Bauerle et al. 1999, Spicer and Gartner, 2001, Meinzer,

2003 and Woddruff et al. 2004). Personal observation of many old Douglas-fir trees with a history of top dieback and re-growth, regaining apical dominance with lateral branches, suggests that this is a common occurrence with this species. Because of the vigor and apparently normal water potential range of the residual foliage observed on Tree 3 (with top dieback) in the cc treatment of the 5-year site, it is possible that as a function of top dieback due to a change in microclimate (Koch et al. 2004) in relation to possible hydraulic height limitations (Ryan and Yoder 1997) there is a compensating (acclimation) effect facilitating the survival of the remaining portion of the tree.

In the 0-year site, relatively low midday water potentials were observed in both treatments. However, water potential of the cc treatment sample trees were frequently lower, reaching potentially damaging levels (Figures 5.4 and Table 5.8). For the 5-year site, differences between trees and treatments for midday and predawn water potentials were not as great (Figure 5.4 and 5.5 and Table and 5.9). The 5-year site cutblock had approximately 30 % standing dead leave-trees when sampled 5-years after harvest. Therefore, it is possible the trees which persist at the older site are the ones that were better able to acclimate with time to the sudden change in their environment after harvest. Thus, they are not as water stressed during moisture demanding periods as trees on the recently logged site. This observation, and the between tree variability seen at both sites for all trees, suggests there may be substantial genetic and/or microsite variability around the trees allowing some to cope more effectively than others. Larger sample sizes will be required in order to test this hypothesis further to determine if mortality of some trees is

merely postponed or if they truly acclimate more successfully than those that die soon after harvest.

Although predawn measurements for each site appear to be quite similar, some trees had lower water potentials than others. For the 0-year site, the most negative mean predawn water potential values occurred for both sample trees in the cc treatment, while at the 5-year site all trees except for one in the cc and one in the un had similar average seasonal predawn water potentials. This suggests trees with the more positive water potential values may be recovering (recharging) more efficiently than the those with the more negative values during the evening while stomata are open and respiration and recharge is taking place (Figure 5.5 and Table 5.11) (Ritchie and Hinckley, 1975, Hinckley et al. 1978, Richter, 1997, Donovan et al. 1999 and Sala et al. 2001).

Tree 1 in the un treatment of the 5-year site appears to have lower midday and predawn twig water potentials than other trees during mid summer and may not be fully recovering during the evening. In the fall of 2003 just before data collection finished for the season, a number of basidiocarps (mushrooms) of *Inonotum tomentosus* root rot appeared in close proximity to the trees in the un treatment particularly tree 1. Henigman et al. (2001) noted that Douglas-fir is susceptible to this pathogen although it is primarily associated with spruce. *I. tomentosus* occurs in a patchy nature associated with moist as opposed to wet or dry sites and is common in mixed stands of spruce and pine where Douglas-fir at this latitude are also often found (Lewis, 1991). Because of its ability to compromise the vascular tissue of the roots, the presence of *I. tomentosus* basidiocarps in close proximity

(50 cm) to the lateral roots of tree 1 in the un may explain observed water potential values that were consistently more negative (greater stress) than expected for trees in an unharvested stand.

It is also plausible that if these trees are infected with root rot they may be likely candidates for early mortality if retained as leave-trees after harvest. Myron and Patton (1971) found that in *Pinus resinosa* (Ait.) stands *I. tomentosus* mortality was much higher in the intermediate versus the dominant crown class. If this pattern is the same for Douglas-fir crown class distributions it may indicate that the larger older trees although root compromised may still be able to cope with a certain level of infection under conditions where the surrounding canopy has not been removed. Figure 5.2 d. shows that combined twig water potential values for the trees in the 5-year un treatment were skewed to the left, illustrating the higher frequency at which these trees attained more negative water potential values than those of the 5-year cc treatment.

Throughout the growing season in both the 0-year and 5-year sites, twig water potentials lower than -3.0 MPa were seen in both unharvested and harvested treatments. However, they occurred more frequently and reached minimum values as low as -3.6 MPa for tree 1 and -4.5 for tree 2 in the cc treatment of the 0-year site. Values less than -3.5 Mpa are unusual for this species and can have negative impacts on xylem conductivity (Bond and Kavanagh, 1999). Douglas-fir is considered to be conservative and does not routinely function near the edge of catastrophic cavitation in stems (Jones and Sutherland, 1991). In Douglas-fir, mean cavitation water potential for small roots has been observed at -2.1

MPa (Sperry and Ikeda, 1997 and Stout and Sala 2003) versus -3.8 MPa for larger roots (Sperry and Ikeda, 1997) and -4.23 for small stems and shoots. Cavitation can lead to loss of turgor resulting in cell death (Comstock, 2002). Cavitation is the point at which the xylem tension exceeds the cohesive force of water and has been measured at around -3.0 MPa (Salisbury and Ross, 1978).

Early spring and late fall revealed very low water potentials for some trees (tree 2 in 0-year site and trees 4 and 2 in 5 year site). It has been suggested that this may be the result of dehydration in the fall and re hydration in the spring, as the trees move in and out of winter dormancy as osmotic potentials become more negative with frost hardiness (Salisbury and Ross, 1978). Thus, detections of low water potentials in late fall and early spring may have more to do with dormancy and frost hardiness than solely with VPD and available water. However, because our measurements did not detect this pattern for all trees, this once more suggests that there is substantial tree to tree variability.

Differences in local microsite environment were considerable between cc and un treatments. Trees in cc treatments at both sites were exposed to greater VPD, had higher % soil moisture content, and higher soil temperatures.

Wind speed, also a factor controlling transpiration rate (Coombs, et al. 1985), was not only greater in the cc treatments at both sites than in the un treatments, but was also significantly greater at the 0-year site than at the 5-year site. An increase in wind speed decreases the boundary layer resistance over leaves increasing evaporation and bringing

leaf temperature closer to air temperature (Coombs, et al. 1985). Because increases in wind speed can be associated with transpirational increases, this suggests that geographical spatial factors such as cutblock exposure may also have an influence on the magnitude of transpirational demand leave-trees are exposed to throughout the season.

Differences between treatments for the 0-year site are significant with higher vapor pressure deficits (Table 5.8). However, this was not the case for the 5-year site (Table 5.9). The *y*-intercept (twig water potential) for a linear model was more negative for the cc than for the un treatment at the 0-year site (Figures 5.6 a, b). This difference again suggests a greater influence of VPD on twig water potential for trees in the cc treatment than those of the un treatment for this site.

VPD has been shown to be an effective environmental parameter associated with stress (Bodapati et al. 1992). Increased biosynthesis and accumulations of solutes such as proline are associated with osmotic stress in plants (Boggess et al, 1976; Stewart, 1981; Rhodes et al, 1986; Rhodes and Handa, 1989). Higher proline levels were observed in four different cultivars of barley (*Hordeum vulgare* L.) that were subjected to high VPD versus the same cultivars under low VPD (Bodapati et al. 1992). When water use of individual interior Douglas-fir trees was measured in two plots at a forest site in southern British Columbia, average daily early summer water use by trees with diameters of 7.5-70 cm varied from 1.8 to 166 L sap flux density (cm^3 water/cm^2 sapwood per hour), and was linearly related to shoot xylem pressure potential and was found to increase with increasing VPD and short-wave irradiance (I), reaching maximum rates with VPD > 0.6

kPa and I > 200 Wm^2 (Simpson, 2000). As shown in Figure 5.16, VPD in clearcuts is greater throughout the season than in unharvested forests. However, the correlation of twig water potential with VPD was weaker (smaller r^2) in the cc treatment than in the un treatment indicating that in the cc treatment there may be other factors substantially contributing to the variability seen in the regression model. Some factors that may contribute to the increase in variability seen in the twig water potential versus VPD relationship for the cc treatment are: i) increased soil moisture content, ii) temperature, and iii) wind speed.

In this study, transpirational demand is presented as a measure of vapor pressure deficit. Although water loss in plants by transpiration is driven by vapor pressure deficit (Gao et al. 2002) a more comprehensive measure of evaporative demand is 'potential evapotranspiration'. This is conceptualized as the rate at which evapotranspiration would occur from a large area completely and uniformly covered with vegetation and having access to unlimited soil water (Dingman, 1994). Bladon et al. (2005) used micrometerological data with the Penman combination equation (Van Bavel, 1996) to provide potential evapotranspiration for sites in a study examining differences in transpiration between three tree species under variable retention harvesting. Included in the Penman equation are: the slope of the saturation vapor pressure versus air temperature curve, net radiation, air density, heat capacity of the air, windspeed, vapor pressure deficit, water density, latent heat of vaporization and the psychrometric constant (Van Bavel, 1996). In studies, particularly where evaporative demand is parameter of

comparison, the use of a method such as the Penman combination equation provides a more accurate measure.

VPD had less influence on twig water potential values at the 5-year site. If the surviving trees in the 5-year cc treatment have successfully acclimated changes in their environment, then the water potential influencing factors described for the 0-year site would not be as important. Seasonal twig water potential values were significantly more positive (less stressed) in the 5-year cc treatment than in the 0-year cc treatment. This suggests some degree of acclimation by the residual trees.

Over the season, VPD between the two sites did not differ considerably, although, the 0-year site did have a slightly higher summed seasonal VPD value. However, as a result of higher stress loading due to more frequent lower water potentials, cumulative water potential values were clearly greater for the trees in the cc treatment of the 0-year site compared to its un treatment, and much greater than that of the 5-year site for predawn and midday. This is possibly a result of insufficient water uptake capacity in relation to a sudden increase in transpirational demand immediately following harvesting of the cutblock.

Questions remain as to whether the observation of higher levels of stress in the cc versus the un treatment of the 0-year site compared to that of the 5-year site were i) a result of time since harvest (e.g. trees capable of acclimation had not yet achieved it at the 0-year site), or ii) a result of differences in micro environment between the two sites (e.g. VPD

and soil temperature were higher at the 0-year site compared to that of the 5-year site). However, the observed mortality (approximately 30-40%) at the 5-year site when sampling took place indicates that the dead trees in the cc treatment were the ones incapable of acclimating quickly enough at this site and may have seen the same trend for lower water potentials immediately after harvest 5-years earlier as those in the cc treatment of the 0-year site did in summer of 2003 immediately after harvest.

5.0 Tables and figures:

Table 5.1. Sample tree descriptions for the un and cc treatments at the 0-year and 5-year sites.

Site	Treatment	Tree	Age (yrs)	Dbh (cm)	Height (m)	% live crown
0-year	UN	1	202	76.7	41.2	50.9
0-year	UN	2	lost	79.6	40.7	66.8
0-year	CC	1	194	96.5	40.0	61.3
0-year	CC	2	309	57.9	37.4	39.8
5-year	UN	1	lost	61.5	34.8	49.4
5-year	UN	2	lost	78.7	33.2	46.4
5-year	CC	1	182	63.3	35.0	52.6
5-year	CC	2	255	63.5	31.3	54.6
5-year	CC	3	118	58.4	21.6	58.3
5-year	CC	4	94	45.8	30.4	41.8

Table 5.2. Example of gravitational height correction derived value used to standardize twig water potential values for all comparable trees to minimum twig removal height (tree with lowest shooting height)

Twig removal height (m)	Height difference from standard (26.6 m)	Gravitational correction value (Bars)	Gravitational correction value (MPa)
39	12.4	1.24	0.124
	e.g. 3.20 MPa - {39 m-26.6 m x -.01) = -3.076 MPa		

Table 5.3. Example of procedure for obtaining statistical estimates for pooled observed proportions and p-values based on the z-statistic.

Observed frequencies for CC treatment						
treatment		tree #	low	normal	high	Total
(A_1)	cc	1	9	35	11	55
cc		2	7	26	19	52
		Total	16	61	30	107
			x1	x1	x1	n1
Observed frequencies UN treatment						
treatment		tree #	low	normal	high	Total
(A_2)	un	1	4	36	6	46
un		2	11	34	3	48
		Total	15	70	9	94
			x2	x2	x2	n2
Proportions (p') of CC and UN						
treatment			low	normal	high	
(B)	cc		0.1495	0.5701	0.2804	
un			0.1596	0.7447	0.0957	
(C)		**P'_p**	0.1542	0.6517	0.1940	
(D)		**z**	-0.1967	-2.5923	3.3027	
(E)		***p*-values**	0.4207	0.0047	0.0005	

Table 5.4. Two-Sample t-Test assuming unequal variances for all seasonal midday and predawn twig water potential sample values between trees 1 and 2 within CC and UN treatments for the 0-year site (α=0.05).

	CC Midday (Mpa)		UN Midday (Mpa)		CC Predawn (Mpa)		UN Predawn (Mpa)	
	Tree 1	*Tree 2*	*Tree 1*	*Tree 2*	*Tree 1*	*Tree 2*	*Tree 1*	*Tree 2*
Mean	-2.23	-2.50	-2.12	-1.93	-0.90	-0.96	-0.83	-0.75
Variance	0.63	0.96	0.43	0.39	0.05	0.04	0.02	0.04
Observations	55	52	46	48	21	21	18	21
Hypothesized Mean Difference	0.00		0.00		0.00		0.00	
Df	98		91		39		36	
t Stat	-1.55		1.40		-1.04		1.37	
P(T<=t) two-tail	0.1248		0.1636		0.3064		0.1794	

Table 5.5. Two-Sample t-Test assuming unequal variances for all seasonal midday and predawn twig water potential sample values between trees 1 and 2 within CC and UN treatments for the 5-year site (α=0.05).

	CC Midday (Mpa)		UN Midday (Mpa)		CC Predawn (Mpa)		UN Predawn (Mpa)	
	Tree 1	*Tree 2*	*Tree 1*	*Tree 2*	*Tree 1*	*Tree 2*	*Tree 1*	*Tree 2*
Mean	-1.8136	-2.0046	-2.2543	-1.9863	-1.0109	-0.8874	-1.1144	-0.9212
Variance	0.1461	0.2899	0.381	0.3251	0.0457	0.025	0.0776	0.0455
Observations	41	42	44	47	21	21	17	21
Hypothesized Mean Difference	0		0		0		0	
df	74		87		37		29	
t Stat	-1.8671		2.1478		2.1276		2.3558	
P(T<=t) two-tail	0.0659		0.0345		0.0401		0.0255	

Table 5.6. Seasonal midday treatment proportions for frequency of occurrences of values in water potential (wp) stress categories (l=low, n=normal, h=high), p-values for level of significance, Ho statements for combined trees in treatments and y/n statement regarding whether cc tree twig values significantly occurred more frequently in high stress (h) water potential category.

Seasonal	Site	Treatment	wp Category	Proportion	*p*-value	Ho accept	Ho reject	Freq. higher in cc high stress (h) wp cat? (y/n)
Seasonal	0-year	cc	l	0.1495				
Seasonal	0-year	un	l	0.1613	0.4207	x		
Seasonal	0-year	cc	n	0.5701				
Seasonal	0-year	un	n	0.7527	0.0035		x	
Seasonal	0-year	cc	h	0.2804				
Seasonal	0-year	un	h	0.086	0.0002		x	y
Seasonal	5-year	cc	l	0.2651				
Seasonal	5-year	un	l	0.1648	0.2266	x		
Seasonal	5-year	cc	n	0.6867				
Seasonal	5-year	un	n	0.7802	0.0668	x		
Seasonal	5-year	cc	h	0.0482				
Seasonal	5-year	un	h	0.0549	0.4207	x		n

Table 5.7. Monthly midday means and standard error for water potential (wp) for individual trees in cc and un treatments for the 0-year and 5-year sites.

Month	Site	Treatment	Tree #	Mean wp (MPa)	SEM
June	0-year	cc	1	-1.77	0.05
June	0-year	cc	2	-2.69	0.66
June	0-year	un	1	-1.83	0.13
June	0-year	un	2	-1.99	0.21
June	5-year	cc	1	-1.78	0.12
June	5-year	cc	2	-1.67	0.09
June	5-year	un	1	-1.99	0.09
June	5-year	un	2	-1.81	0.18
July	0-year	cc	1	-2.56	0.27
July	0-year	cc	2	-2.61	0.39
July	0-year	un	1	-1.95	0.32
July	0-year	un	2	-2.04	0.31
July	5-year	cc	1	-2.14	0.18
July	5-year	cc	2	-2.04	0.15
July	5-year	un	1	-2.61	0.21
July	5-year	un	2	-2.13	0.23
August	0-year	cc	1	-2.85	0.52
August	0-year	cc	2	-2.58	0.45
August	0-year	un	1	-2.55	0.31
August	0-year	un	2	-2.08	0.13
August	5-year	cc	1	-1.81	0.20
August	5-year	cc	2	-2.25	0.10
August	5-year	un	1	-2.48	0.24
August	5-year	un	2	-2.27	0.12
Sept-Oct	0-year	cc	1	-2.1	0.53
Sept-Oct	0-year	cc	2	-2.17	0.69
Sept-Oct	0-year	un	1	-2.12	0.48
Sept-Oct	0-year	un	2	-1.74	0.50
Sept-Oct	5-year	cc	1	-1.53	0.19
Sept-Oct	5-year	cc	2	-1.97	0.44
Sept-Oct	5-year	un	1	-1.95	0.48
Sept-Oct	5-year	un	2	-1.83	0.46

Table 5.8. Seasonal midday treatment proportions for frequency of occurrences of values in water potential (wp) stress categories (l=low, n=normal, h=high), p-values for level of significance, Ho statements for combined trees in treatments and y/n statement regarding whether cc tree twig values significantly occurred more frequently in high stress (h) water potential category low VPD range (< 1.2 KPa) and high vpd range (> 1.2 KPa) for the 0-year site.

VPD grouping	Site	Treatment	wp Category	Proportion	*p*-value	Ho accept	Ho reject	Freq. higher in cc high stress (h) wp cat? (y/n)
low	0-year	cc	l	0.03				
low	0-year	un	l	0.08	0.1375	x		
low	0-year	cc	n	0.95				
low	0-year	un	n	0.92	0.3821	x		
low	0-year	cc	h	0.03				
low	0-year	un	h	0.00	0.1357	x		n
high	0-year	cc	l	0.00				
high	0-year	un	l	0.00	n/a			
high	0-year	cc	n	0.43				
high	0-year	un	n	0.84	0.0002		x	
high	0-year	cc	h	0.57				
high	0-year	un	h	0.16	0.0002		x	y

Table 5.9. Seasonal midday treatment proportions for frequency of occurrences of values in water potential (wp) stress categories (l=low, n=normal, h=high), p-values for level of significance, Ho statements for combined trees in treatments and y/n statement regarding whether cc tree twig values significantly occurred more frequently in high stress (h) water potential category Low VPD range (< 1.2 KPa) and High vpd range (> 1.2 KPa) for the 5-year site.

VPD grouping	Site	Treatment	wp Category	Proportion	*p*-value	Ho accept	Ho reject	Freq. higher in cc high stress (h) wp cat? (y/n)
low	5-year	cc	l	0.32				
low	5-year	un	l	0.09	0.0122		x	
low	5-year	cc	n	0.68				
low	5-year	un	n	0.85	0.0606	x		
low	5-year	cc	h	0.00				
low	5-year	un	h	0.06	0.0968	x		n
high	5-year	cc	l	0.03				
high	5-year	un	l	0.00	0.1587	x		
high	5-year	cc	n	0.97				
high	5-year	un	n	0.94	0.2912	x		
high	5-year	cc	h	0.00				
high	5-year	un	h	0.06	0.1251	x		n

Table 5.10. Comparison between the 0-year and 5-year sites for differences in seasonal midday treatment proportions for frequency of occurrences of values in water potential (wp) stress categories (l=low, n=normal, h=high), p-values for level of significance, Ho statements for combined trees in treatments.

Site	Treatment	wp Category	Proportion	*p*-value	Ho accept	Ho reject
0-year	cc	l	0.15			
5-year	cc	l	0.27	0.0256		x
0-year	cc	n	0.57			
5-year	cc	n	0.69	0.0495		x
0-year	cc	h	0.28			
5-year	cc	h	0.05	0.0001		x
0-year	un	l	0.16			
5-year	un	l	0.16	0.4801	x	
0-year	un	n	0.75			
5-year	un	n	0.78	0.3264	x	
0-year	un	h	0.09			
5-year	un	h	0.05	0.2119	x	

Table 5.11. Seasonal mean values and standard error for midday and predawn sample trees in the cc and un treatments for the 0-year and 5-year sites.

Time sector	Site	Treatment	tree #	Mean	SEM	CI (95%)	*n*
Midday	0-year	cc	t1	-2.23	0.11	-2.23 ± 0.21	55
Midday	0-year	cc	t2	-2.50	0.14	-2.50 ± 0.27	51
Midday	0-year	un	t1	-2.12	0.10	-2.12 ± 0.19	46
Midday	0-year	un	t2	-1.93	0.09	-1.93 ± 0.18	48
Midday	5-year	cc	t1	-1.81	0.06	-1.81 ± 0.12	41
Midday	5-year	cc	t2	-2.00	0.08	-2.00 ± 0.16	42
Midday	5-year	cc	t3	-2.07	0.05	-2.07 ± 0.10	24
Midday	5-year	cc	t4	-2.24	0.10	-2.24 ± 0.20	45
Midday	5-year	un	t1	-2.25	0.09	-2.25 ± 0.18	44
Midday	5-year	un	t2	-1.99	0.09	-1.99 ± 0.19	44
Predawn	0-year	cc	t1	-0.90	0.05	-0.90 ± 0.10	21
Predawn	0-year	cc	t2	-0.96	0.04	-0.96 ± 0.08	21
Predawn	0-year	un	t1	-0.83	0.03	-0.83 ± 0.06	18
Predawn	0-year	un	t2	-0.75	0.04	-0.75 ± 0.08	21
Predawn	5-year	cc	t1	-1.01	0.05	-1.01 ± 0.09	21
Predawn	5-year	cc	t2	-0.89	0.03	-0.89 ± 0.07	21
Predawn	5-year	cc	t3	-0.90	0.03	-0.90 ± 0.05	21
Predawn	5-year	cc	t4	-0.90	0.03	-0.90 ± 0.07	21
Predawn	5-year	un	t1	-1.12	0.06	-1.12 ± 0.13	18
Predawn	5-year	un	t2	-0.92	0.05	-0.92 ± 0.09	21

Table 5.12. Daily mean midday tree twig water potentials (n=3), standard error and VPD for midday sampling at the 0-year site.

Date	t1 cc	t1 sem	t2 cc	t2 sem	t1 un	t1 sem	t2 un	t2 sem	VPD
6-Jun	-1.81	0.08	-4.53	0.09	-1.68	0.01			no data
13-Jun	-1.72	0.02	-2.05	0.19	-1.7	0.06	-1.67	0.04	1.2
27-Jun	-1.78	0.01	-2.12	0.03	-2.11	0.02	-2.31	0.05	1.2
4-Jul	-1.74	0.06	-1.88	0.12	-1.86	0.10	-1.48	0.15	0.2
14-Jul	-2.84	0.04	-2.84	0.26			-2.01	0.03	1.3
17-Jul	-2.71	0.04	-2.07	0.18	-1.68	0.02	-1.69	0.12	1.3
22-Jul			-3.24	0.25					1.7
24-Jul	-2.59	0.12	-2.98	0.13	-1.61	0.12	-2.11	0.03	0
31-Jul	-2.91	0.20	-3.41	0.21	-3.02	0.13	-2.91	0.10	3.4
7-Aug	-3.34	0.10	-3.28	0.22	-2.46	0.09	-1.89	0.02	1.5
11-Aug	-0.98	0.03							1.1
14-Aug	-3.59	0.16	-2.82	0.14	-2.76	0.10	-2.36	0.03	1.7
22-Aug	-1.79	0.03	-1.62	0.04	-2.58	0.53	-2.01	0.08	0.4
3-Sep	-2.45	0.57	-2.92	0.19	-2.44	0.13	-2.99	0.25	2.2
8-Sep	-2.51	0.08	-2.69	0.07	-2.53	0.12	-2.07	0.13	0.9
18-Sep	-2.61	0.07	-2.25	0.07	-1.87	0.08	-1.27	0.30	0.4
25-Sep	-3.18	0.16	-3.81	0.08	-3.13	0.06	-2.37	0.04	no data
29-Sep	-2.33	0.03							no data
7-Oct	-0.86	0.06	-0.62	0.02	-0.69	0.08	-0.77	0.07	no data
17-Oct	-1.13	0.05	-0.71	0.03	-1.94		-0.99	0.02	no data

Table 5.13. Daily mean midday tree twig water potentials (n=3), standard error and VPD for midday sampling the 5-year site.

Date	t1 cc	t1 sem	t2 cc	t2 sem	t4 cc	t4 sem	t1 un	t1 sem	t2 un	t2 sem	VPD
9-Jun	-2.03	0.12			-4.07	0.46	-1.98	0.14	-1.48	0.02	1.2
12-Jun	-1.75	0.09	-1.78	0.07	-1.85	0.03	-1.89	0.08	-1.89	0.18	1.5
26-Jun	-1.65	0.03	-1.57	0.04	-2.32	0.02	-2.09	0.08	-2.09	0.07	0.6
3-Jul	-1.87	0.14	-1.82	0.14	-1.91	0.04	-2.14	0.05	-1.67	0.09	1.4
18-Jul	-2.03	0.04	-2.1	0.11	-1.88	0.03	-2.77	0.02	-1.89	0.04	1.9
19-Jul	-2	0.05			-2.03	0.27					0.9
24-Jul	-2.6	0.05			-2.28	0.11	-2.86	0.31	-2.46	0.08	0.2
31-Jul	-2.25		-2.2	0.15	-2.28	0.09	-2.66	0.06	-2.49	0.07	2.3
7-Aug			-2.38	0.09	-2.6	0.09	-2.07	0.04	-2.17	0.06	1.2
15-Aug	-2.13	0.09	-2.07	0.00	-2.47	0.26	-2.79	0.12	-2.11	0.03	3
18-Aug	-1.9	0.05									1.5
22-Aug	-1.43	0.04	-2.32	0.08	-2.58	0.17	-2.54	0.24	-2.52	0.02	0
3-Sep		0.02	-1.9		-2.55	0.03	-2.82	0.02	-2.51	0.28	2.7
10-Sep	-1.33	0.07	-1.95	0.04	-1.85	0.13	0		-2.22	0.07	0.4
19-Sep	-1.86	0.02	-2.5	0.06	-2.55	0.09	-2.31	0.18	-2.64	0.27	no data
25-Sep	-2.2		-3.2	0.11			-2.42	0.19	-1.92	0.06	no data
29-Sep	-1.53	0.03									no data
8-Oct	-1.18	0.06	-1.27	0.03	-1.48	0.07	-1.13	0.23	-1.06	0.06	no data
17-Oct			-1.02	0.06	-1	0.09	-0.79	0.03	-0.66	0.00	no data

Table 5.14. Monthly and seasonal mean, max., min. and sum 'local area' site level VPD values for daily times between 1100 and 1300 hours for the 0-year site.

VPD (KPa)	May	June	July	August	September	Seasonal
Mean	0.88	1.18	1.41	1.35	0.68	1.14
SEM	0.04	0.05	0.07	0.06	0.07	0.03
StdDev	0.53	0.65	0.82	0.69	0.68	0.72
Sum	135.42	174.01	218.31	209.89	59	796.63
Max	2.35	2.66	3.6	3.72	2.66	3.72
Min	0	0	0.02	0	0	0
n	154	147	155	155	87	698

Table 5.15. Monthly and seasonal mean, max., min. and sum 'local area' site level VPD values for daily times between 1100 and 1300 hours for the 5-year site.

VPD (KPa)	May	June	July	August	September	Seasonal
Average	1.25	1.31	1.45	1.32	0.66	1.25
SEM	0.09	0.06	0.07	0.06	0.08	0.03
StdDev	0.61	0.74	0.89	0.72	0.72	0.81
Sum	53.82	192.99	224.26	204.87	57.59	733.52
Max	2.76	3.43	3.83	3.78	2.69	3.83
Min	0.07	0	0	0	0	0
Count	43	147	155	155	87	587

Table 5.16. Mean and daily maximum wind speed (m/s) for cup anemometers in the cc at the 0-year site and the cc and un treatments of the 5-year site from June 15 to July 28, 2006.

Treatment	5 yr cc	5 yr un	0 yr cc
n=days	37	37	85
Mean (m/s)	2.37	1.33	2.84
Daily max (m/s)	3.33	1.78	4.62
StdDev	0.31	0.17	0.45
SEM	0.05	0.03	0.05

Figure 5.1. Geographic location of Study area within the Prince George timber supply area. In 2002 sampling took place in both the Ft. St. James and Prince George Forest Districts indicated by the upper and lower arrows and in 2003 in the Prince George Forest District only.

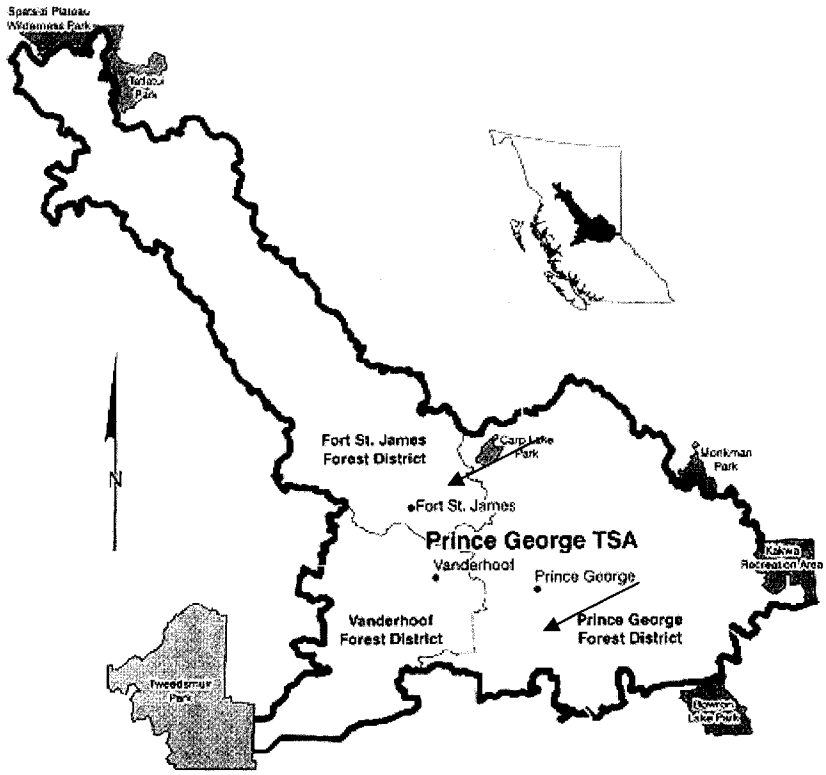


Figure 5.2. Distribution histograms for seasonal twig water potential values for combined trees in: a) 0-year cc treatment, b) 0-year un treatment, c) 5-year cc treatment and d) 5-year un treatment.

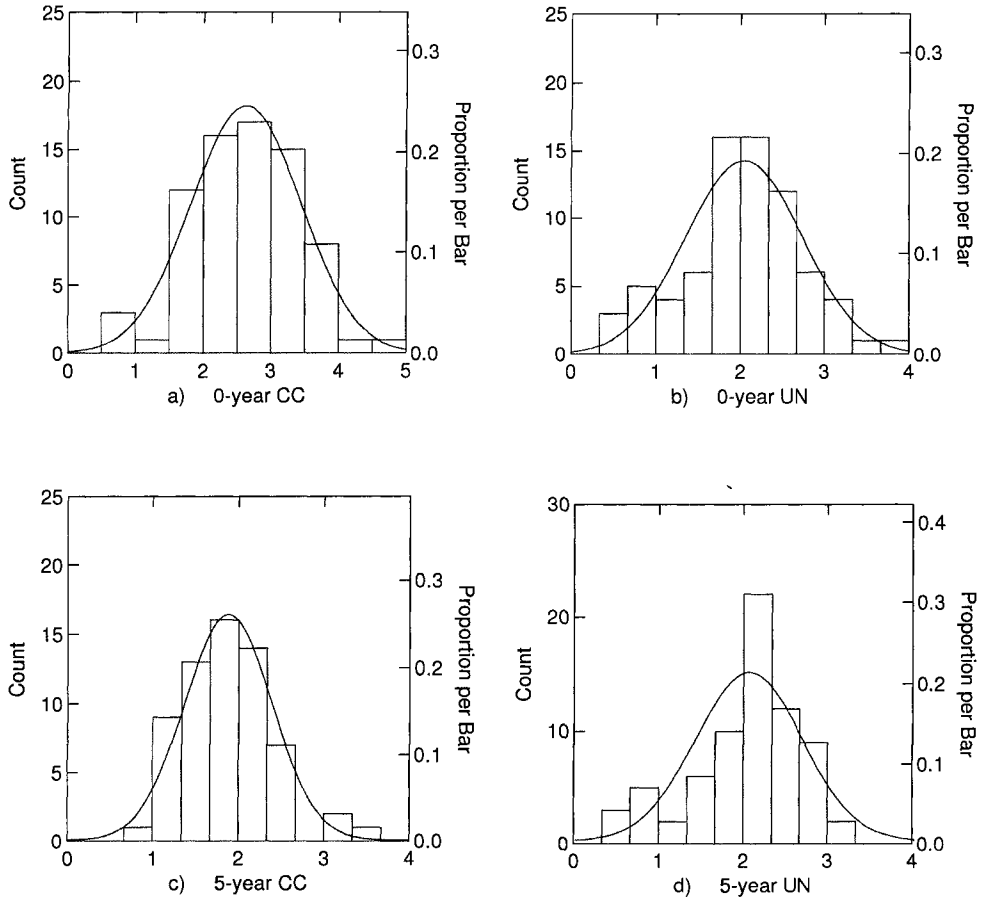


Figure 5.3. Percent occurrence of twig midday values for all trees in both cc and un sites that fell into three water potential stress categories (low, normal and high).

Block age	Treatment	Tree #	total twigs (n)	≥ -1.6 (MPa) Low %	≤ -1.61 ≥ -2.9 (MPa) Normal %		Total %
0-year	cc	1	55	16	64	20	100
0-year	cc	2	52	13	50	37	100
0-year	un	1	45	9	80	11	100
0-year	un	2	48	23	71	6	100
5-year	cc	1	41	34	63	2	100
5-year	cc	2	42	19	74	7	100
5-year	cc	3	24	96	4	0	100
5-year	cc	4	45	13	80	7	100
5-year	un	1	44	11	82	7	100
5-year	un	2	47	21	74	4	100

Figure 5.4. Midday seasonal mean twig water potential values for trees in unharvested and harvested treatments for 0-year and 5-year sites.

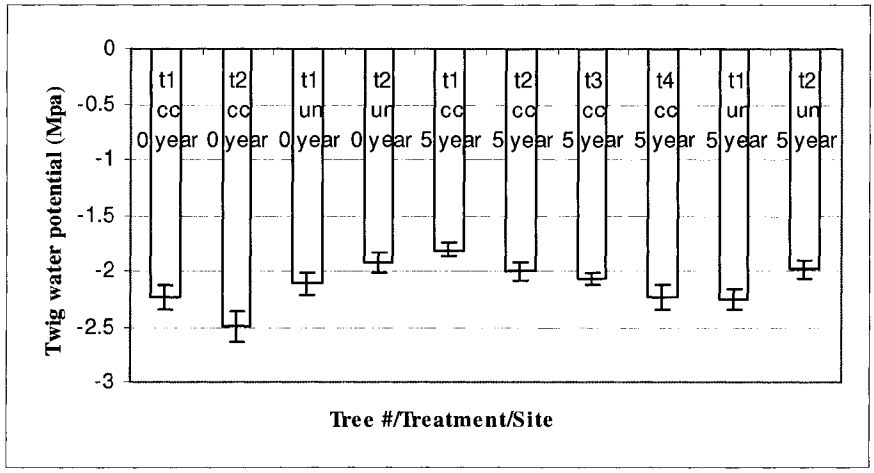


Figure 5.5. Predawn seasonal mean twig water potential values for trees in unharvested and harvested treatments for 0-year and 5-year sites.

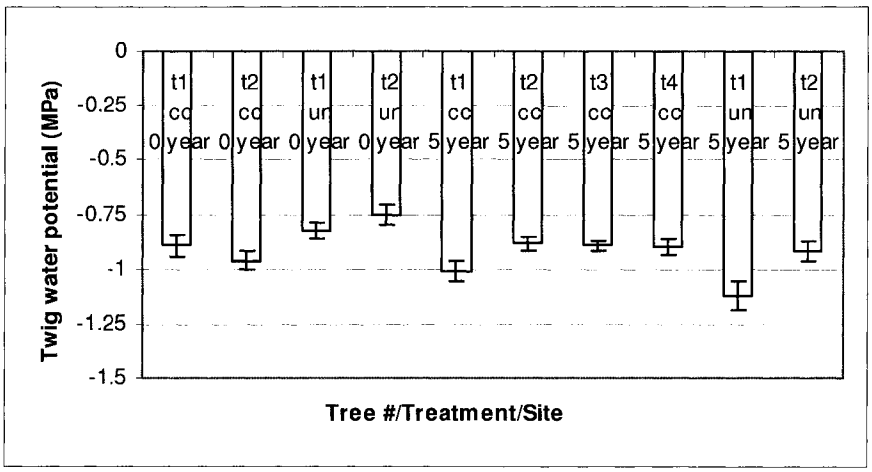
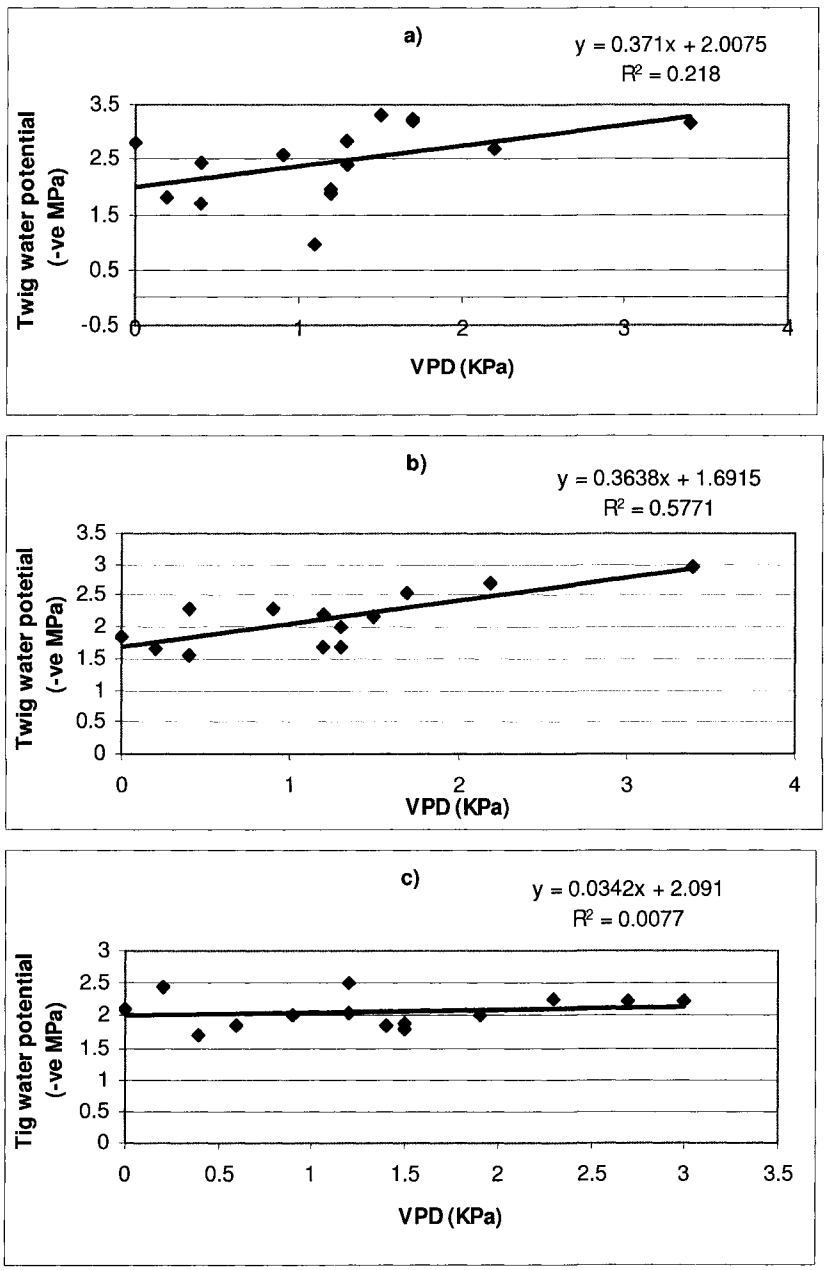


Figure 5.6. Linear regressions for twig water potential with VPD as an independent variable against the corresponding daily values for the dependent variable twig water potential for a) 0-year site cc treatment, b) 0-year site un treatment, c) 5-year site cc treatment and d) 5-year site un treatment.



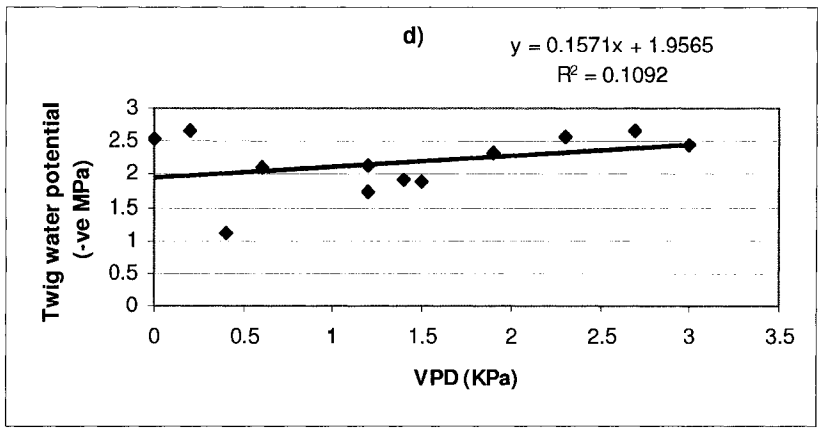


Figure 5.7. Midday daily tree mean twig water potential values for trees in unharvested and harvested treatments for the 0-year site. The symbols represent individual trees and are arranged vertically on the graph by sample date. Occasionally some days have only one value taken as a reference for ancillary sampling.

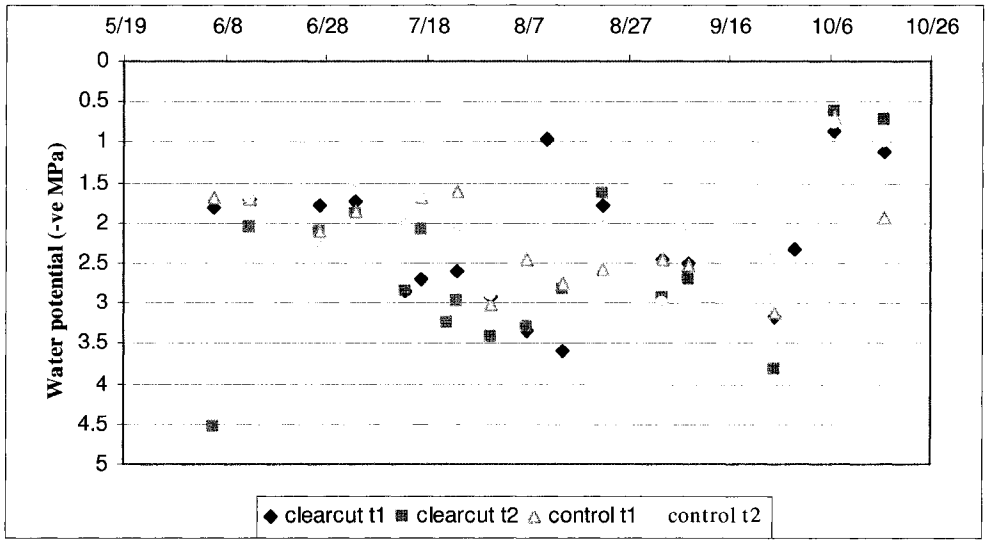


Figure 5.8. Midday daily tree mean twig water potential values for trees in unharvested and harvested treatments for the 5-year site. The symbols represent individual trees and are arranged vertically on the graph by sample date. Occasionally some days have only one value taken as a reference for ancillary sampling.

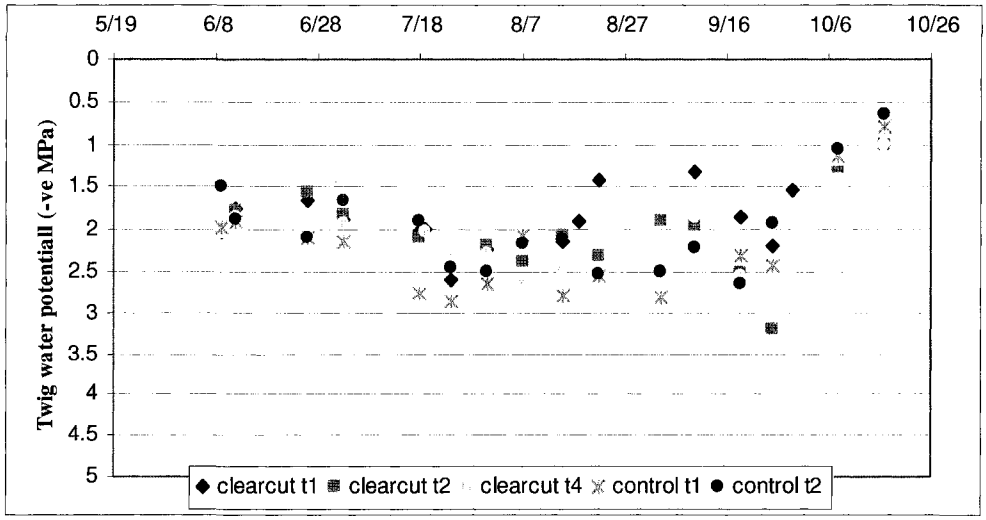


Figure 5.9. Predawn daily tree mean twig water potential values for trees in unharvested and harvested treatments for the 0-year site. The symbols represent individual trees and are arranged vertically on the graph by sample date. Occasionally some days have only one value taken as a reference for ancillary sampling.

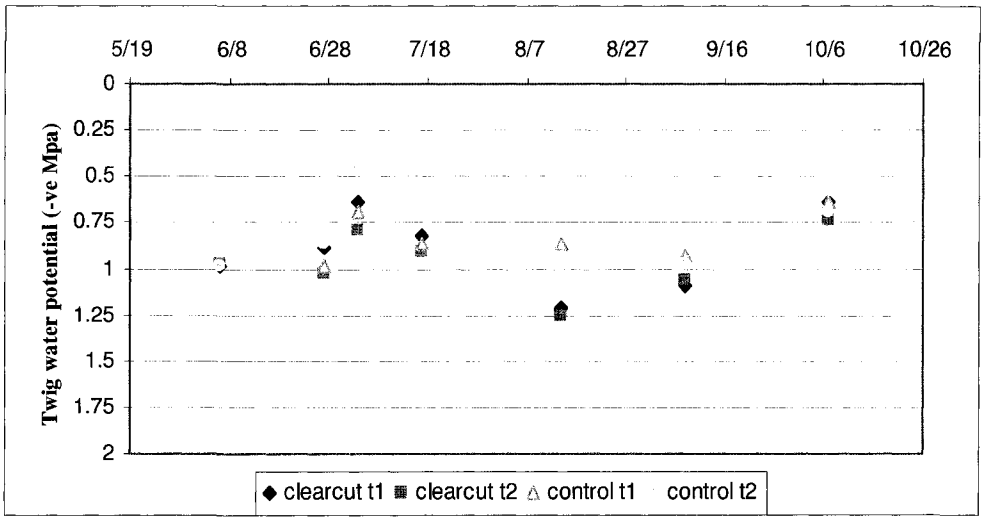


Figure 5.10. Predawn daily tree mean twig water potential values for trees in unharvested and harvested treatments for the 5-year site. The symbols represent individual trees and are arranged vertically on the graph by sample date. Occasionally some days have only one value taken as a reference for ancillary sampling.

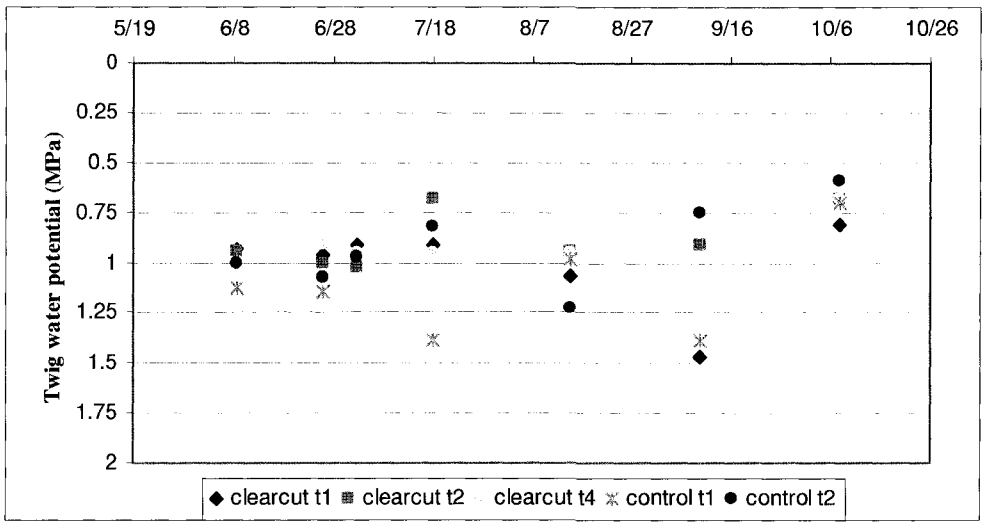


Figure 5.11. Cumulative seasonal midday twig water potential values for the 0-year site.

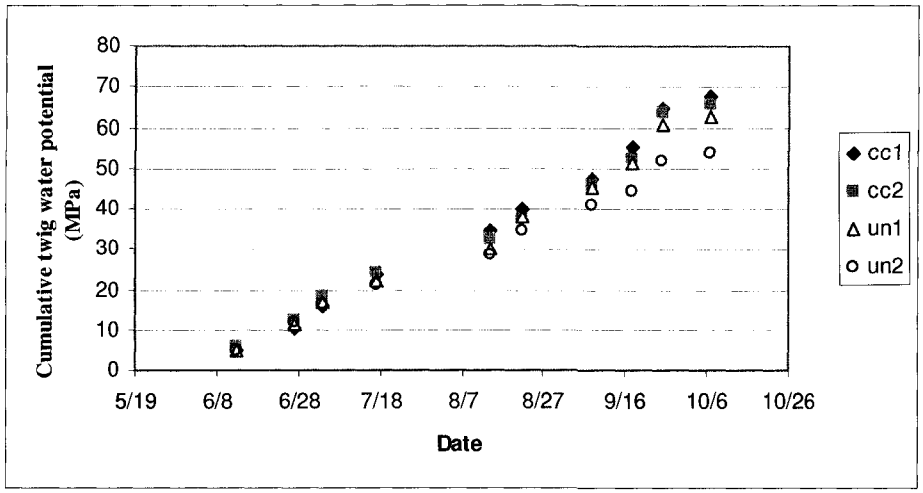


Figure 5.12. Cumulative seasonal midday twig water potential values for the 5-year site.

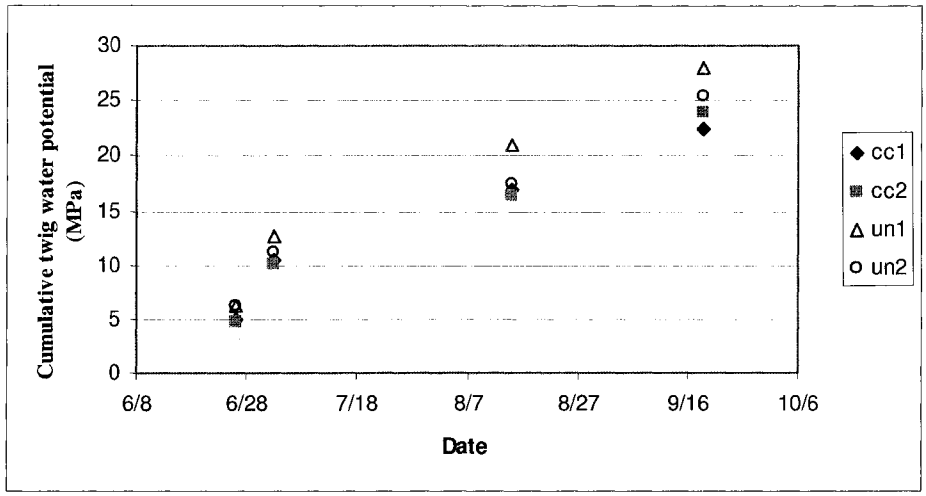


Figure 5.13. Cumulative seasonal predawn twig water potential values for the 0-year site.

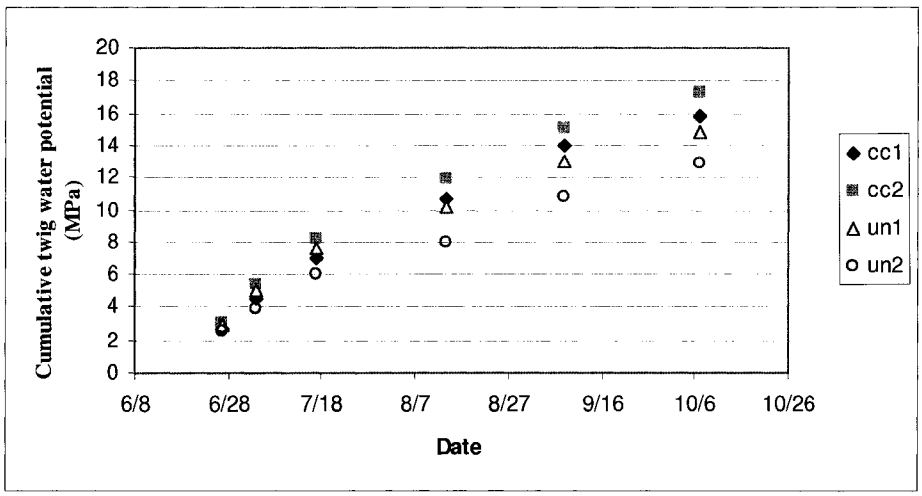


Figure 5.14. Cumulative seasonal predawn twig water potential values for the 5-year site.

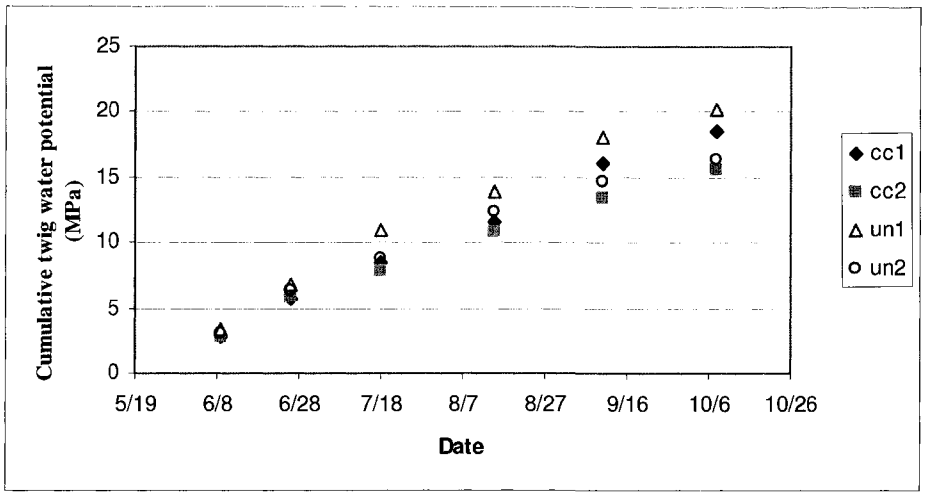


Figure 5.15. Daily mean wind speed for the 5-year site cc and un treatments and for the 0-year site cc treatment for the sample season.

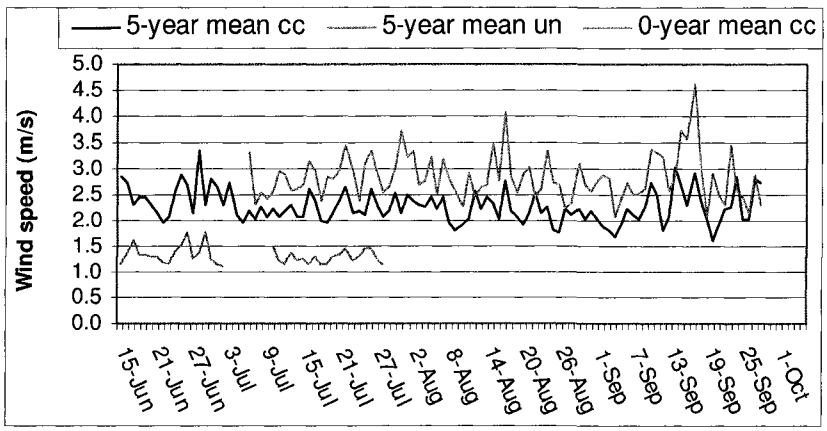
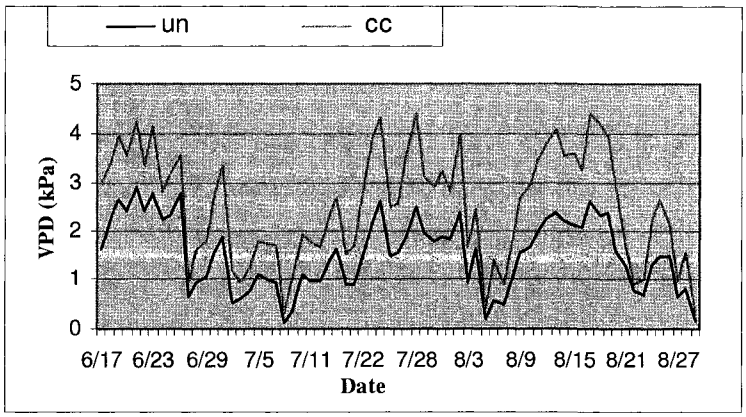


Figure 5.16. 2004 seasonal representation of daily maximum VPD values (KPa) for un and cc treatments in the SBSdw3/mk1 subzone.



6.0 Plant and soil water relations: 2) Soil moisture and temperature

6.1 Introduction

It is plausible soil conditions following forest harvesting may have adverse effects on leave-tree roots and thus whole tree hydraulic conductivity. This may in turn contribute to postharvest loss of vigor and eventually to mortality. Many aspects of plant water use, particularly in response to soil drought, may be the result of the alteration of hydraulic conductance from soil to canopy (Sperry et al. 2002). The capacity to conduct water from soil to leaves is an important regulatory factor of leaf level gas exchange (Mencuccini, 2003). Although stomatal aperture directly controls water loss to the atmosphere, it does so by incorporating information about both the availability of soil water and the efficiency of the plant water transport system. If this did not happen, stomata could not effectively balance carbon uptake against water loss (Mencuccini, 2003). Stomata are responsive to hydraulic conductance changes along the flow path from soil to leaf (Hubbard et al. 2002).

Stomata have also shown response to experimental root pruning (Sperry and Pockman 1993), which simulates root dieback. Lu and Neumann (1999) examined the mechanisms by which moderate water stress (adding polyethylene glycol 6000 to the root medium) induces a sustained inhibition of hydraulic conductivity and leaf growth in rice (*Oryza sativa* L.) seedlings: the inhibition of leaf growth correlated well with the induced water stress.

When leaf area, soil moisture, predawn leaf water potential, and sap flow were examined in three Douglas-fir stands of 20, 40 and approximately 500-years in age, Bond et al. (1999) found that soil moisture became more depleted during the growing season in the younger stands compared to the old-growth. Predawn water potential measurements of understory species also showed a trend of more rapid depletion of soil moisture in the youngest stand compared to the oldest. When the sap flow of whole trees was divided by total leaf area for the whole tree to produce an estimate of unit leaf transpiration, the flux rates for the two age classes appeared nearly identical when soil moisture was high and just slightly higher for younger trees when soil moisture was low (Bond et al. 1999). This is a consequence of the much lower leaf area per unit sapwood area in the older trees. But it is also important to note that soil moisture availability was much lower in the younger stand on each of these days meaning that the young trees were able to "pull" water from soil more effectively than the older trees. When the same data are expressed as a function of VPD rather than time, it is clear that the older tree's transpirational response to soil water deficit was greater than in younger trees (e.g. the stomatal response to VPD was more sensitive and occurred sooner in older than younger trees) (Bond et al. 1999). The objective of this element of the study is to determine whether differences exist among sites and between cc and un treatments for soil moisture and temperature.

6.2 Methods

At the time of midday water potential sampling, soil moisture was also measured at each tree and periodically along transects in each treatment throughout the sampling season

with a soil moisture meter using Time Domain Reflectometery (TDR) technology (E.S.I. Environmental Sensors Inc., Moisture Point®, MP-917).

Four, 30 cm TDR soil moisture probes were fixed under the drip line around each sample tree. Probes were also placed horizontally on a 10 cm, 30 cm and 60 cm vertical profile in a soil pit at each tree. Each soil pit was covered with a teepee tarp while not in use, with the vertical soil surface containing the TDR probes also covered with plastic garbage bags to avoid excess moisture accumulation and excess evaporation. Each TDR point sample consisted of recording three soil moisture content (% volume) measurements with a time delay reading. Point samples were averaged for each tree. Where sample trees were close together and soil texture and drainage characteristics similar, soil moisture measurements from one sample point were used for both trees in a treatment. Line transects in the clearcut and unlogged areas were established with TDR sample points every 50m and ran between the sample trees into the cutblock. Each site had 7 points in the cc treatment and 4 points in the un treatment. At the 5-year site they were measured during the first part of the growing season to establish site variability as well as differences between treatments. Equations using time delay values were used to correct (calibrate) some data during data summary (Herkelrath, 1991; Hook and Livingston 1996). Soil temperature was also measured in each of the treatments throughout the sampling season at both sites using thermocouples buried at 10cm, 30cm and 60cm depths in the soil pit. Data were recorded on Campbell Scientific® CR10X data loggers.

6.3 Results

6.3.1 Soil moisture

Mean soil moisture point measurements taken from line transect data in cc and un treatments to capture treatment variability at both sites showed a general trend for higher soil moisture content in the cc treatment than in the un treatment throughout the season (Figures 6.1 and 6.2). Relative differences between treatments in the 0-year site are slightly greater than those in the 5-year site for sample days where line transects were used, ranging from 7.3-10.6 % in the 0-year site to 4.7 to 7.8 % in the 5-year site.

Volumetric soil moisture content (%) vertical profiles at 10 cm, 30 cm and 60 cm depths in the 0-year site trends for increasing moisture content with depth are clear and more pronounced in the cc than in the un treatment (Figure 6.3). As with the transect treatment values overall moisture content was greater in the cc than in the un treatments. For the 0-year site cc and un treatments, the June 24, July 31 and August 14 daily snapshots all showed a trend for increasing soil moisture with increasing depth (Figure 6.3). In the 5-year cc and un treatments this trend was only seen in June (Figure 6.3).

6.3.2 Soil temperature

Soil temperature decreased from 10 cm to 30 cm to 60 cm for both sites and was generally higher at all depths in the cc treatments throughout the growing season (Figures

6.4 – 6.7). Highest daily maximum values were seen at the 0-year site in the cc treatment (20.9 C). At the 5-year site the highest daily maximum values were seen in the cc treatment (16.9 C) versus the un treatment (15.5 C) (Figure 6.8).

6.4 Discussion

Both sites maintained greater moisture content in the cc treatments compared to that of the un treatments, with greater relative differences between the cc and un seen in June and July at the 0-year site. Higher soil temperatures were also maintained at both sites in cc treatments compared to the un treatments. In general, the cc treatment of the 0-year site maintained a higher soil temperature profile having the highest daily maximum values throughout the sampling season compared to that of the cc treatment at the 5-year site (Figures 6.8). Increases in soil temperature can result in significant evaporation (Brady, 1990) in the top 20 cm of soil where most fine roots responsible for water uptake exist (Herman, 1997). This results in fine root dieback (Hendrick and Pregitzer, 1993 and Pregitzer et al. 1997) and increased soil acidification which limits available cations (Tomlinson, 1992).

Total vegetation cover was substantially greater around the sample trees at the 5-year site compared to that of the 0-year site. For the 5-year site, shrub cover was three times that of the 0 year site (Table 6.1). This is likely to have two effects: i) more vegetation would result in more of the sun's radiation being absorbed and reflected, resulting in lower soil temperatures; and 2) a greater percentage of deeper rooting shrubs at the 5-year site

(Table 6.1) would have resulted in more of the water in the cc treatment being utilized in comparison to the 0-year site, thus resulting in roots being exposed for less time to the excess water in the cutblock. If higher soil temperatures in conjunction with higher soil water content can potentially have negative effects on fine root survival and production (Hendrick and Pregitzer, 1993 and Pregitzer et al. 1997), water up take would be limited (reduced) while transpirational demand would be increased over that of the preharvest conditions. These factors in conjunction with varying degrees of hydraulic limitation (Ryan and Yoder 1997 and Sperry et al. 2001) would negatively impact Douglas-fir leave-trees.

6.0 Table and figures:

Table 6.1. Site descriptions (cc= clearcut).

Site	Subzone	Site series	Land form	Soil text	Seral stage	Surf shape	cc % herb cover	cc % shrub cover	cc total % veg cover
0 yr	SBSdw3/dw2	01	Glacial till	Sandy loam	Mature seral	Flat/gentle roll	6	1.5	7.5
5 yr	SBSdw3	01/06	Glacial till	Sandy loam	Mature seral	Flat/gentle roll	9	12	21

Figure 6.1. Mean volumetric soil moisture content (%) with standard error bars for cc and un treatments on line transects at the 0-year site.

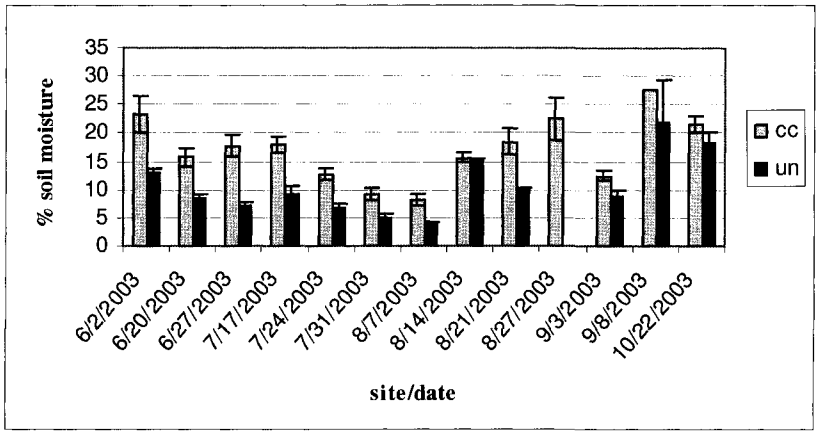


Figure 6.2. Mean volumetric soil moisture content (%) with standard error bars for cc and un treatments on line transects at the 5-year site.

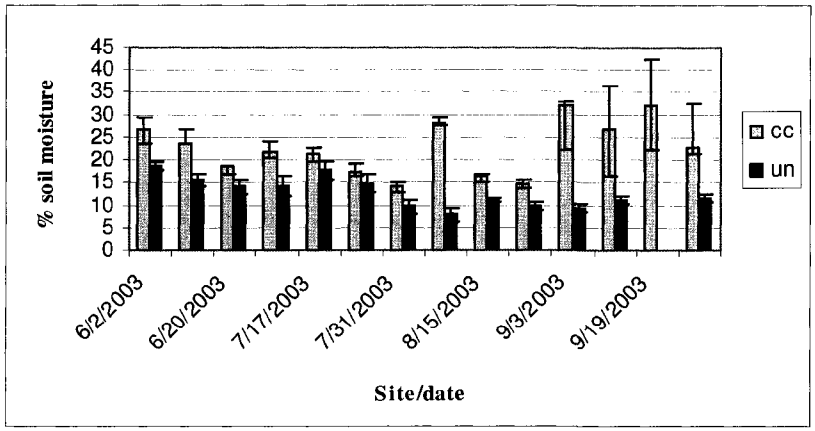


Figure 6.3. 0-year (0-Y) and 5-year (5-Y) site volumetric soil moisture content (%) with standard error bars at 10cm, 30cm and 60cm depths on June 24, July 31 and August 14 (0-Y) and August 7 (5-Y), 2003.

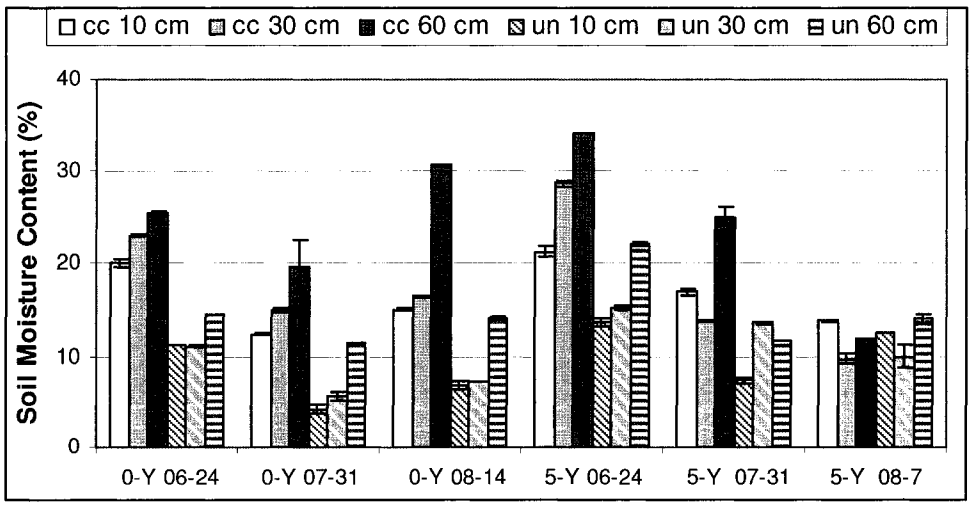


Figure 6.4. Daily maximum soil temperature values at 10 cm, 30 cm and 60 cm depths for the 0-year site cc treatment

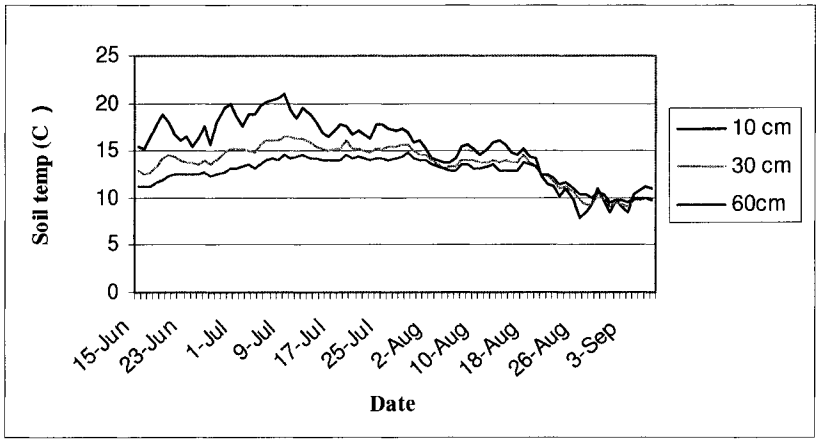


Figure 6.5. Daily maximum soil temperature values at 10 cm, 30 cm and 60 cm depths for the 5-year site cc treatment.

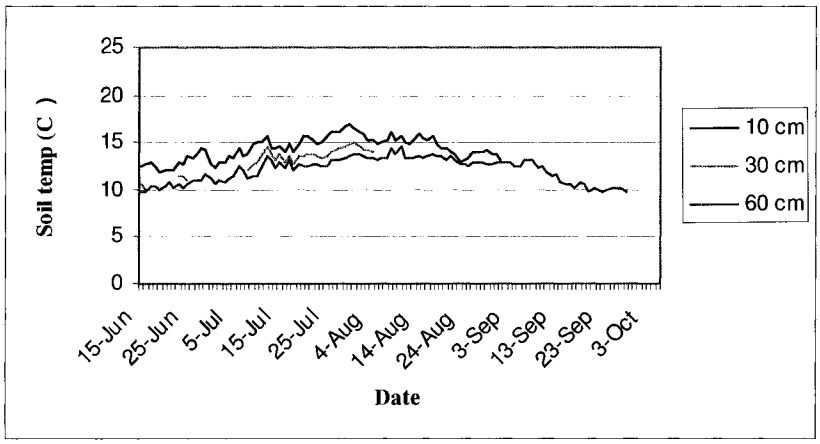


Figure 6.6. Daily maximum soil temperature values at 10 cm, 30 cm and 60 cm depths for the 5-year site un treatment

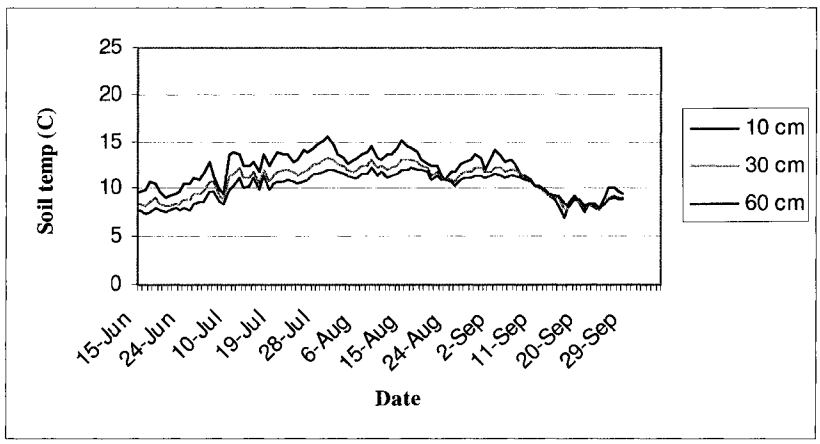


Figure 6.7. Daily maximum soil temperature values at 10 cm depth for the 5-year site cc and un treatments.

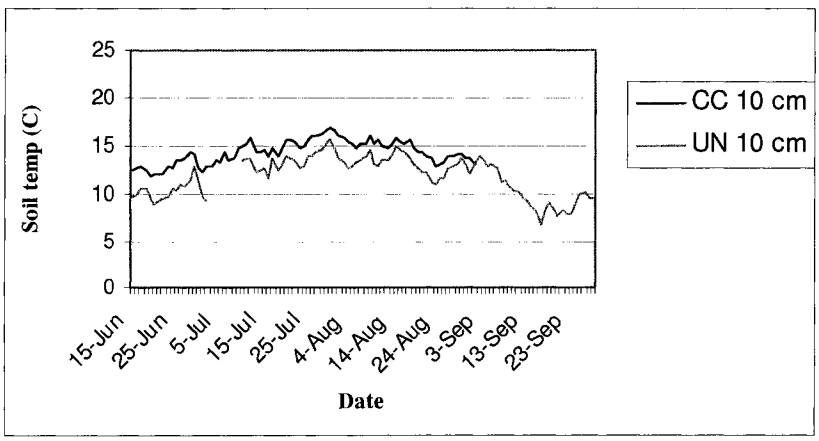
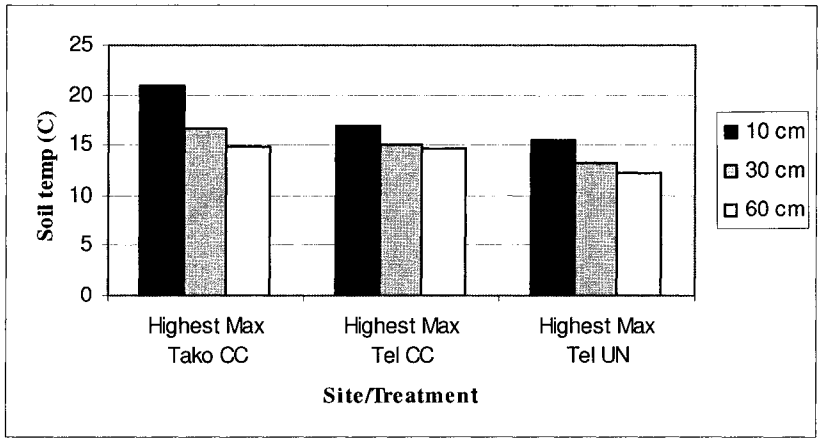


Figure 6.8. Highest daily maximum soil temperature values at 10 cm, 30 cm, and 60 cm depths for the 0-year cc, 5-year cc and 5-year un treatments.



7.0 Stable carbon isotope $^{13}C/^{12}C$ ratios

7.1 Introduction

Stable $^{13}C/^{12}C$ isotope ratios ($d^{13}C$) were measured for Douglas-fir leave-trees in harvested versus unharvested units in 2003 and 2004 to determine relative water stress. $d^{13}C$ can be used as an indicator of water stress because it is in part a reflection of the temporal dynamics of stomatal response to transpirational demand and soil water availability. Thus it is indicative of plant water use efficiency and variable $^{13}CO2$ and $^{12}CO2$ fixation and assimilation into plant tissue.

Leaf carbon isotope discrimination reflects the ratio of leaf internal to external CO_2 (^{13}C and ^{12}C) concentration and is an integrated, long term measure of the effect of factors such as stomatal closure due to water stress affecting inward diffusion (leaf conductance) and CO_2 consumption (photosynthetic rate) (Farquhar et al. 1989; Ehleringer et al. 1993). It is expected that these factors will vary between the cc and un Douglas-fir leave-tree treatments and thus carbon isotope discrimination should as well.

Carbon isotope discrimination ($\Delta^{13}C$) and ratio ($d^{13}C$) is a method for examining water use efficiency in plants. It has been used widely (Farquhar et al. 1989; Bond, et al 1999; Cregg and Zhang 2000; Bowling, et al. 2002; McDowell, et al. 2003; McDowell, et al. 2004). The amount of isotopic discrimination that occurs during assimilation may be compared by $\Delta^{13}C$ or $d^{13}C$). The magnitude that plants discriminate against the heavier

carbon isotope ^{13}C during CO_2 fixation depends on the photosynthetic pathway (C_3, C_4 or CAM), and on the ratio of the concentration of CO_2 inside the leaf and in ambient air. The latter is controlled by stomatal conductance (g) and assimilation rate (A) (Farquhar et al. 1982; Sheidegger et al. 2000). As presented in equation 6, the A/g ratio is called intrinsic water use efficiency (WUE) and in C_3 plants it is proportional to $d^{13}C$ of the primary photosynthetic products, where:

$$6)\ d^{13}C = 1000\ [\frac{(^{13}C/^{12}C)\ \text{sample}}{(^{13}C/^{12}C)\ \text{standard}} - 1]$$

Bowling et al. (2002) found a non linear relationship between ecosystem respired $d^{13}C$ and vapor pressure deficit along a precipitation gradient for a variety of conifer forests. These findings supported traditional concepts of stomatal influence over $\Delta^{13}C$ at the leaf level. Sparks and Ehleringer (1997) found that several *Populus* species discriminated less against ^{13}C at higher elevations due to a decrease in leaf-air vapor pressure difference. If this were the case, then one would expect that Douglas-fir leave-trees in clearcut treatments exposed to higher vapor pressure deficits more frequently throughout the growing season would discriminate more against ^{13}C too.

The normal rate of diffusion of $^{13}CO_2$ across the stomatal pore is lower than that of $^{12}CO_2$ by a factor of 4.4 parts per-thousand (‰). There is also an isotope effect caused by the preference of ribulose bisphosphate carboxylase (*Rubisco*) for $^{12}CO_2$ over $^{13}CO_2$ (by a factor of ~27‰). In both cases, the processes discriminate against the heavier isotope ^{13}C (Farquhar et al. 1989). Based on the work of Farquhar the linkage between discrimination against ^{13}C during photosynthesis and water use efficiency may be demonstrated by the following relationships. The stable isotope ratio ($d^{13}C$) is expressed

as the $^{13}C/^{12}C$ ratio relative to a standard (Pee Dee Belemnite[6]) (Craig 1957). The resulting $d^{13}C$ value (equation 7) may be used to estimate isotope discrimination $\Delta^{13}C$ as:

7) $\Delta^{13}C = (d_a - d_p)/(1+ d_p)$

where d_p is the isotopic composition of the plant material and d_a is that of the air (assumed to be 8 ‰). As CO_2 assimilation (A) increases or stomatal conductance (g_s) decreases, intercellar CO_2 decreases resulting in decreased discrimination against ^{13}C.

The relationship between c_i and $\Delta^{13}C$ as represented by the model of Farquhar et al. (1982) in equation 8:

8) $\Delta^{13}C = 4.4 + 22.6(c_i/c_a)$

where c_i is the intercellular CO_2 and c_a is atmospheric CO_2 ($\approx$ 355 ppm).

Intra- and inter-specific variations in leaf values have been correlated with a diversity of related gas exchange components, including leaf conductance, hydraulic conductivity, water-use efficiency, and photosynthetic capacity (Woodward 1986; Körner et al. 1988; Farquhar et al. 1989; Ehleringer et al. 1993). Abiotic factors, such as soil moisture availability and humidity, have also been shown to exert a significant influence on leaf isotope values (Winter et al. 1982; Madhavan et al. 1991; Ehleringer et al. 1993).

This portion of the study was carried out under the working hypothesis that trees, in part due to differences in vapor pressure deficit between treatments, would exhibit seasonal $d^{13}C$ signatures reflecting this. Thus, the objectives of this study are: 1) to determine if differences in $d^{13}C$ exist between trees in harvested versus unharvested treatments, and 2)

---

[6] Doucett 2004. For carbon, the international standard is Pee Dee Belemnite, a carbonate formation, whose generally accepted absolute ratio of $^{13}C/^{12}C$ is 0.0112372.

whether those trees also exhibited the most negative (indicating water stress) water potential values.

7.2 Methods

In the fall of 2003 and 2004, wood and leaf samples were taken respectively, from large old Douglas-fir leave-trees in cc and unharvested un treatment units for analysis of stable carbon isotope ratios ($d^{13}C$). In 2003, wood samples from radial increments were collected from 2 trees in each treatment at 2 sites (cutblocks) in the drier portion of the SBS biogeoclimatic (BEC) zone of central British Columbia, one harvested 5-years earlier (5-year site) and on the previous winter (0-year site). In 2004, the 2003 study was continued. However, instead of wood samples, leaf samples were utilized. The study was also expanded to examine the response of Douglas-fir $d^{13}C$ across a precipitation gradient. This was achieved by sampling in three progressively wetter BEC zones; the SBS mk1, wk1 and vk1. Five sites were sampled using the site and tree selection methods presented in chapter 5; two in the SBSmk1 (0-year and 5-year), two in the SBSwk1 (0-year and 6-year) and one in the SBSvk1 (1-year). The 0-year site in the SBSdw2 from 2003 was originally going to be sampled as well but unfortunately the 2 sample trees in the cc treatment were both wind-thrown in the 2003-04 winter and subsequently could not be included in the 2004 sampling.

For the 2004 sites, twig water potentials were measured for all sample trees using the methodology described in chapter 5 for comparison with the $d^{13}C$ values.

7.2.1 2003 Wood Samples

Tree cores were taken from each sample tree at breast height in September of 2003. The wood was then separated into pre and postharvest sections for both sites; 2003 (post) and 2002 (pre) for the 0-year site and 2003 and 1998 (post) and 1997 (pre) for the 5-year site. Rings were separated in the lab under a dissection microscope with the use of a scalpel. The samples were then freeze dried and placed in sterile containers. Ring samples were then sent to the University of British Columbia's stable isotope laboratory where they were crushed to powder and mass spectrometry measurements were taken for $d^{13}C$ (Leavitt and Danzer, 1993; Livingston and Spittlehouse, 1996; McDowell et al. 2003)

7.2.2 2004 Needle Samples

In 2004, 0-year old and 5-6 year old sites were sampled in the SBSmk1 and wk1 and a 0-year site in the SBSvk1 just north of Prince George, British. In late September, at the close of the 2004 growing season, twig samples were removed from within the top 5 m of all sample trees using a shot gun. Current year needles were selected from close to the current year's growth node to ensure they were the first to emerge at bud break and had been photosynthetically active the longest. Dried leaf samples were sent to UBC's stable isotope laboratory for analysis. To avoid ecophysiological differences between sun and shade leaves, such as differences in foliar nitrogen and chemical activity observed in *P. menziesii* var. *glauca* (Nippert and Marshal, 2003), all needles collected were sun leaves from representative, older Douglas-fir which are dominant in these forest canopies.

Vapor pressure deficit was also measured at the SBSmk1 0-year site from June to September with the intent of modeling the trend seen at this site across the other sites.

7.3 Results for carbon isotope discrimination

7.3.1 2003 Wood sample

Pre02 (2002 preharvest ring) and post03 (2003 postharvest ring) $d^{13}C$ values (Figure 7.1) at the 0-year site were not as expected. Comparison of $d^{13}C$ pre and postharvest for individual trees in the cc treatment showed more positive (indicating higher stress) values for pre02 wood than post03 wood. Tree number 1 (t1) in the unharvested treatment showed the most positive values (pre02 and post03) of all trees. In the cc treatment at the 5-year site (Figure 7.2), pre97 (1997 peharvest ring) and post98 (1998 postharvest ring) values showed the expected trend having more positive postharvest values for both sample trees 1 and 2. Values from post03 showed even more positive $d^{13}C$ values for each of these trees. It was difficult to compare between un and cc treatments because trees were quite variable.

7.3.2 2004 Leaf samples

2004 leaf sample results indicate that trees in the cc treatments achieved the most positive (lower level of discrimination indicating water stress) $d^{13}C$ values, and that in general

many of the trees across treatments and sites had values indicating water stress (Figures 7.3 – 7.7).

When considering only the SBSmk1 and SBSwk1 0-year sites and the SBSvk1 1-year site, all of which had reasonable numbers of sample days (13, 14 and 11 respectively) in comparison to the SBSmk1 5-year and SBSwk1 6 year sites which had only 3 sample days each, 5 of the 6 sample trees in the cc treatments had more positive (representing greater water stress) $d^{13}C$ values than those in the un treatments. Four of then 6 trees reached lower water potential values (more negative) than -2.90 MPa more frequently than those in the un treatments, 3 of which coincided with the most positive $d^{13}C$ values (Table 7.1)

Within and among needle replication for all individual trees was cost prohibitive. Therefore, measurement error and needle variability for $d^{13}C$ was examined on an arbitrarily chosen tree for among needle variation (n=6) in the SBS mk1 un treatment and within needle variation for the same tree (n=3), along with a tree from the SBSwk1 cc treatment (n=3) and SBSvk1 cc treatment (n=3). Variability within and between needle samples for a single tree in each subzone variant is presented in Table 7.2.

At all five sites, at least one tree in the cc treatment had the most positive (indicative of stress) $d^{13}C$ values (Figures 7.3 to 7.7 and Table 7.1). Values ranged from -23.51 ‰ in the cc treatment for the wettest SBSvk1 subzone (Figure 7.4) to -28.40 ‰ in the un treatment of the driest SBSmk1 subzone examined (Figure 7.7). Trees in the cc treatment

at the 1 year since harvest SBSvk1 site were substantially more positive than those in the un treatment (Figure 7.3). The recently harvested 0-year site in the SBSwk1 also showed more positive values in the cc treatment (Figure 7.4). Although the most positive value was found in the cc treatment at the SBSwk1 5-year site, the other tree in the cc treatment also showed the most negative (least stressed) $d^{13}C$ (Figure 7.5). In the SBSmk1 0-year site cc treatment one tree had the most positive while the other had the most negative $d^{13}C$ of both treatments (Figure 7.6). Finally, in the SBSmk1 5-year site the most positive value was measured in the cc while the most negative value was seen in the un treatment.

7.4 Discussion

It was expected that more positive (indicative of higher stress) $d^{13}C$ values in postharvest cc treatments than in preharvest or un treatments would be observed (Farquhar et al. 1989; Bond, et al 1999; Cregg and Zhang 2000; Bowling, et al. 2002; McDowell, et al. 2003;McDowell, et al. 2004). Although this wasn't the case for the 2003 wood samples, the 2004 leaf samples appear to follow the hypothesized trend. However, lack of replication due to cost limits inference from this data.

Replication for $d^{13}C$ leaf samples was absent in this study in both 2003 and 2004. Lack of statistical analysis of variability among leaf samples subsequently limits the power of inference. However, trends for greater water stress seen in this portion of the of the study

in 2004 for trees in the cc treatments versus those of the un treatments do appear to support the findings presented in chapter 5 seen for water potential values.

There are several possible explanations of why pre02 (2002 postharvest ring) and post03 (2003 preharvest ring) $d^{13}C$ values for sapwood samples at the 0-year site were not as expected. $d^{13}C$ values are reflective of the seasonal climate, therefore, when comparing these values between years it is likely that annual weather pattern introduces considerable variation in individual tree response for $d^{13}C$. This makes it difficult to make definitive conclusions. Because both *A* and *g* are influenced by climate, $d^{13}C$ of plant material has been used as a proxy for environmental conditions during assimilation (Leavit and Long, 1982, 1986; Schleser 1992; Gleixner et al. 1993, 1998 and Jaggi et al. 2002). In particular, the $d^{13}C$ of cellulose has been used as a proxy for climate record at various temporal resolutions, because it is progressively deposited in the annual rings of trees (Leavit and Long, 1982, 1986; Schleser 1992; Gleixner et al. 1993, 1998 and Jaggi et al. 2002). In addition to climate, post photosynthetic fractionation associated with downstream primary and secondary metabolism can alter the isotopic composition of plant material (Leavit and Long, 1982, 1986; Schleser 1992; Gleixner et al. 1993, 1998 and Jaggi et al. 2002). The signature of $d^{13}C$ in tree rings therefore reflects the influences of both climate and intrinsic physiological process (Schultz et al. 2004). In this study, for the 2003 wood samples, early wood and late wood were homogenized for mass spectral analysis. This may have confounded results with a mixed seasonal influence. Some of the $d^{13}C$ in the different tissues would have been under the influence of the previous year's growing season on the current year's sapwood growth. Most studies of $d^{13}C$ have

used bulk organic matter, however, it is now widely understood that bulk organic matter is a weighted mean average of different types of organic matter, each having its own isotope composition (van Bergen and Poole, 2002). Intra-annual sampling of tree rings has usually involved separating latewood from earlywood to obtain a clear inter-annual signal rather than using bulked organic matter (Wilson and Ginsted 1977; Bender and Berge 1982; Hemming et al. 2001; Jaggi et al. 2002). The isotopic signature of late wood tends to be closely correlated with weather of the current year, whereas that of the early wood tends to be closely correlated with the climate conditions of the previous year (Hill et al. 1995). Therefore the two woods could have counteracted each other in the 0-year samples. Given the size of these trees, separation of early and late wood was not practical because annual growth rings were very small (e.g. 0.3 mm).

Discrimination may be strongly dependant on variation in environmental drivers such as atmospheric vapor pressure deficit, photosynthetically active radiation and air temperature that control canopy-scale-stomatal conductance and photosynthesis (McDowell, et al. 2004). 2004 climate station data collected at the SBSmk1 0-year site (intended to model expected trends in all subzones) show considerably higher vapor pressure deficit throughout the sampling season in the cc treatment compared to that of the un treatment (Figure 4.14).

Whether using wood or leaf samples, comparisons of year to year $d^{13}C$ will ultimately be affected by seasonal weather patterns. Differences among sites in $d^{13}C$ for *Pinus greggii* Engelm. in central Mexico were explained by differences in precipitation and altitude,

which influence water status and gas exchange processes (Garcia-G, et al. 2004). Changes in soil water potential matched differences in $d^{13}C$ and there was a significant correlation between $d^{13}C$ and mean annual temperature (Garcia-G, et al. 2004). For both the 0-year and 5-year sites, substantially higher levels of soil moisture were observed in the cc treatment in comparison with the un treatment throughout the sampling season (Figures 6.1 and 6.2).

VPD which is greater in the harvested units versus unharvested forest (Figure 5.16) has an influence on $d^{13}C$. A strong link was found between $d^{13}C$ (ecosystem reparation) in Douglas-fir, and the vapor pressure deficit 5 to 10 days earlier, with freezing events causing a significant deviation from the $d^{13}C$ relationship resulting in higher than expected $d^{13}C$ values. (Bowling, et al. 2002). Across study sites in western Oregon that included Douglas-fir forests, mean annual precipitation varied from 227 to 2,760 mm. Overall $d^{13}C$ (carbon isotope ratio) varied from -23.1 ‰ (more positive value=higher relative drought stress) to -33.1 ‰ (more negative value=lower relative drought stress) respectively (Bowling, et al. 2002).

In the unharvested stand, leaves of the older dominant and co-dominant Douglas-fir are typically one to two thirds shaded. Due to differences in ecophysiology of sun and shade leaves (Nippert and Marshal 2003), it is conceivable that when the canopy is opened up exposing the lower canopy shade leaves to more water demanding microclimate, water stress may occur. Figure 4.14 illustrates that vapor pressure deficit is considerably greater for the shade leaves in the cc treatment compared to that of the un treatment.

Increasing vapor pressure deficit typically causes a reduction in somatal conductance (Cowan, 1994; Hinckly and Braatne, 1994; Montieth, 1995; Oren et al. 1999). Consequently the supply of atmospheric CO_2 to the stomatal pore is reduced, thereby causing the ratio of atmospheric to internal or sub-stomatal CO_2 to decline (McDowell, et al. 2004). Re-fixing of respired carbon can affect the carbon isotope signal of understory foliage (Cregg and Zhang 2000). In forest stands, CO_2 concentrations increase near the ground due to efflux of soil respired CO_2 (Cregg and Zhang 2000). The isotopic composition of respired air differs from the bulk atmosphere (Cregg and Zhang 2000).

The extent to which vertical gradients of $d^{13}C$ exist in foliage depend on a number of stand and climatic factors (Cregg and Zhang 2000). For example, the greater the mixing and turbulence within a stand, the less opportunity there is for gradients to develop. Open stands or stands in exposed areas will have greater air mixing and less likely to have $d^{13}C$ gradients. Brooks et al. (1997) estimated that 20% of the variation in $d^{13}C$ gradient in a canopy of boreal conifers was due to variation in the isotopic composition of the source air. Another possible explanation for the lack of expected treatment effect in the 2003 wood samples at the 5-year site is that the trees that remained living had over time undergone sufficient foliar and root acclimation in response to their new environment.

Site to site comparisons can also be difficult due to local environmental differences. Genetic differences in $d^{13}C$ were found among populations of *Pinus contorta* from wetter coastal sites and drier interior sites. Greater productivity in these populations indicates

that their lower discrimination against $^{13}CO_2$ probably results from higher photosynthetic capacity, not lower stomatal conductance (Guy and Holowachuk, 2001). Although stomatal conductance has a major influence on carbon isotope discrimination and hence $d^{13}C$, variation in carbon allocation must also be considered along with genetic differences associated with environmental site conditions. Therefore, differences in values between sites cannot be conclusively attributed to any treatment effect without first controlling for site effects, which would be extremely difficult if not impossible to achieve. There did not appear to be a subzone moisture gradient effect between sites. However, with few sample trees and high tree to tree variability within treatments it cannot be ruled out. The SBSvk1 (the wettest site sampled) did have the most positive $d^{13}C$ in the cc treatment compared to the other sites measured in 2004 and also had water potential values that fell below -2.90 MPa in the cc treatment more frequently than any of the other sites.

In conclusion, the 2003 wood sample $d^{13}C$ data appear to be confounded for a number of reasons including physiological carbon fractionation and differences in seasonal carbon allocation, along with influences from seasonal climatic variability. Another potential contributing factor to the 2003 observations is the pathological activity in tree 1 of the un treated unit at the at the 5-year site. The pathological activity was not observed until after sampling. Later it was confirmed that this tree was situated in the middle of an area affected by *Inonotus tomentosus* (root disease). This may have lead to greater water stress. Although usually associated with spruce, this pathogen can affect Douglas-fir too (Henigman, et al. 2001).

Due to potentially confounding processes such as post-photosynthetic fractionation of carbon altering the isotopic composition wood and the influence of the climatic conditions of the growing season previous to the year of sampling on early and late wood carbon allocation, leaf (needle) samples appeared to provide results more indicative of immediate seasonal water relations. Leaf samples are also easier to process, as wood samples would need to have early and latewood separated, a tedious process and may not result in complete separation of tissue.

7.0 Tables and Figures:

Table 7.1. $d^{13}C$ (‰) values, frequency of water potential values < -2.90 MPa (%), yes/no statements for i) cc treatment d13C values more positive than un treatment and ii) twig water potential values < -2.90 more frequently in the cc treatment than the un treatment for trees in recent and older cutblocks in the SBSmk1, wk1 and vk1.

Subzone	Block age	Treatment	Tree number	n (sample days)	n (twigs)	$d^{13}C$ (‰)	Frequency of water potential values < -2.90 MPa (%)	cc $d^{13}C$ values more positive than un	Twig values < -2.90 MPa more frequent in cc than un
SBSmk1	0-year	cc	1	13	39	-27.41	15	n	y
SBSmk1	0-year	cc	2	13	35	-24.62	34	y	y
SBSmk1	0-year	un	1	13	39	-26.73	8		
SBSmk1	0-year	un	2	13	38	-25.34	8		
SBSmk1	5-year	cc	1	3	9	-26.59	22	y	y
SBSmk1	5-year	cc	2	3	9	-24.69	22	y	y
SBSmk1	5-year	un	1	3	9	-28.40	11		
SBSmk1	5-year	un	2	3	9	-26.67	22		
SBSwk1	0-year	cc	1	14	39	-27.60	8	y	n
SBSwk1	0-year	cc	2	14	42	-27.54	7	y	n
SBSwk1	0-year	un	1	14	40	-27.72	5		
SBSwk1	0-year	un	2	14	40	-27.63	23		
SBSwk1	6-year	cc	1	3	9	-27.60	11	n	y
SBSwk1	6-year	cc	2	3	9	-25.58	0	y	n
SBSwk1	6-year	un	1	3	9	-26.85	0		
SBSwk1	6-year	un	2	3	9	-26.36	0		
SBSvk1	1-year	cc	1	11	39	-23.51	33	y	y
SBSvk1	1-year	cc	2	11	41	-24.77	27	y	y
SBSvk1	1-year	un	1	11	41	-27.16	12		
SBSvk1	1-year	un	2	11	39	-27.34	5		

Table 7.2 Within and among needle comparisons for variability for a selected tree in each of the SBSmk1, wk1 and vk1 subzone variants.

Site	Treatment	Tree	Comparison	Mean (‰)	n	SD	SEM
mk1-0-year	un	2	among needles	-24.92	6	0.33	0.13
mk1-0-year	un	2	within needle	-24.48	3	0.46	0.26
wk1-0-year	cc	2	within needle	-27.69	3	0.27	0.16
vk1-0-year	cc	1	within needle	-24.17	3	0.64	0.37

Figure 7.1. SBSdw3, 0-year site $d^{13}C$ values for pre02 and post03 in the cc and un treatments.

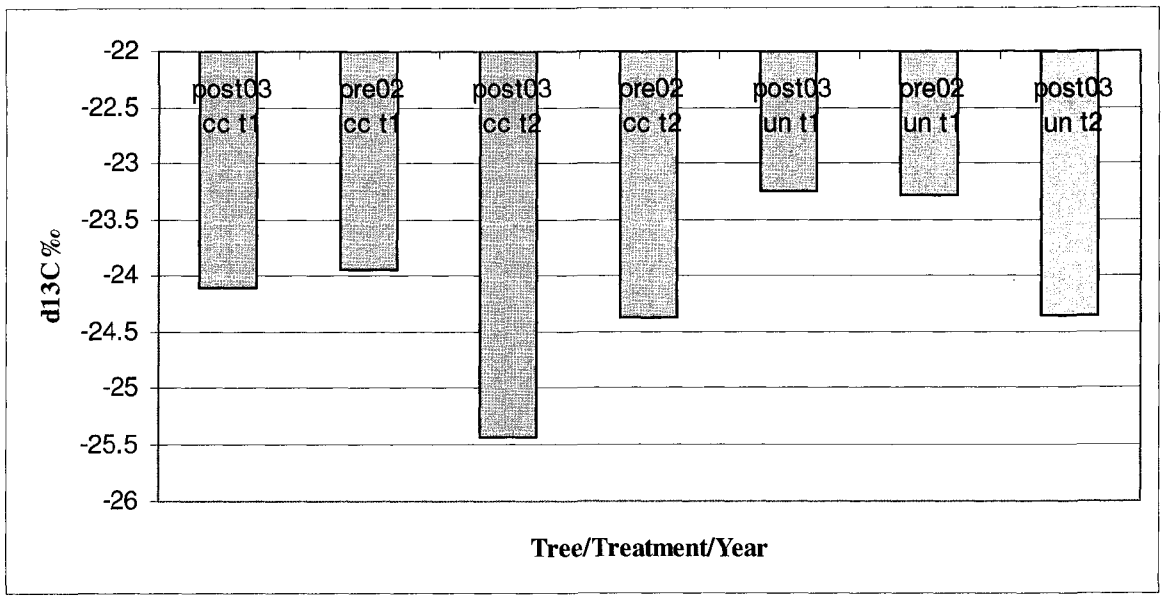


Figure 7.2. SBSdw3, 5-year $d^{13}C$ values for pre97, post98 and post03 in the cc and un treatments.

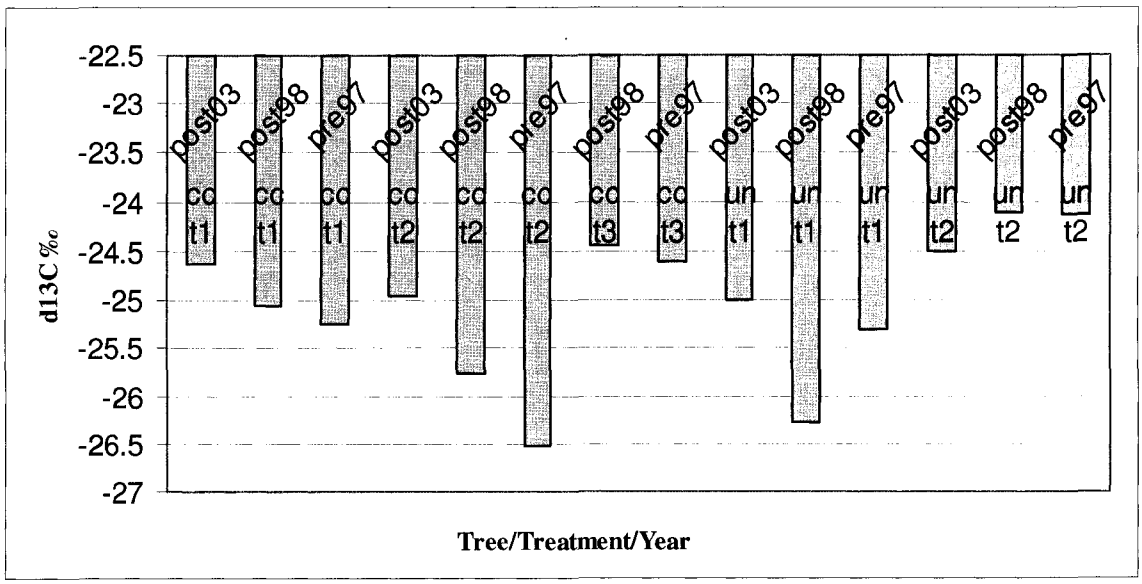


Figure 7.3. SBSvk, 1-year site $d^{13}C$ values for the cc and un treatments.

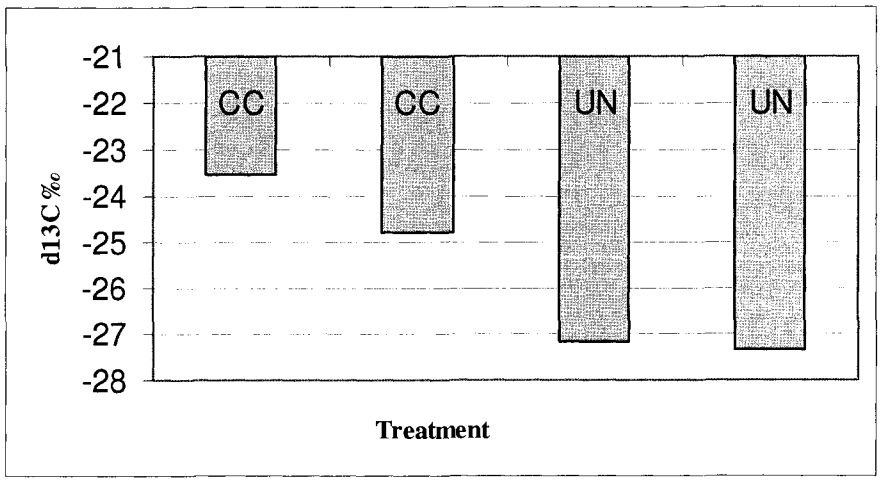


Figure 7.4. SBSwk, 0-year site $d^{13}C$ values for the cc and un treatments.

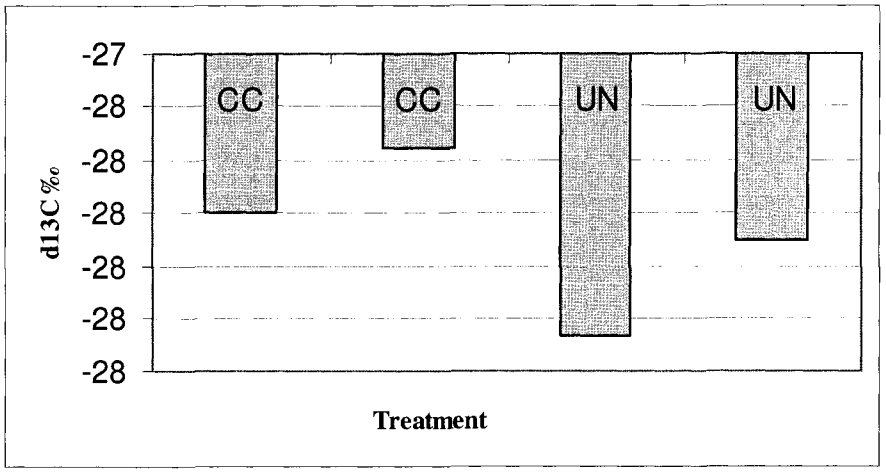


Figure 7.5. SBSwk1, 5-year site $d^{13}C$ values for the cc and un treatments.

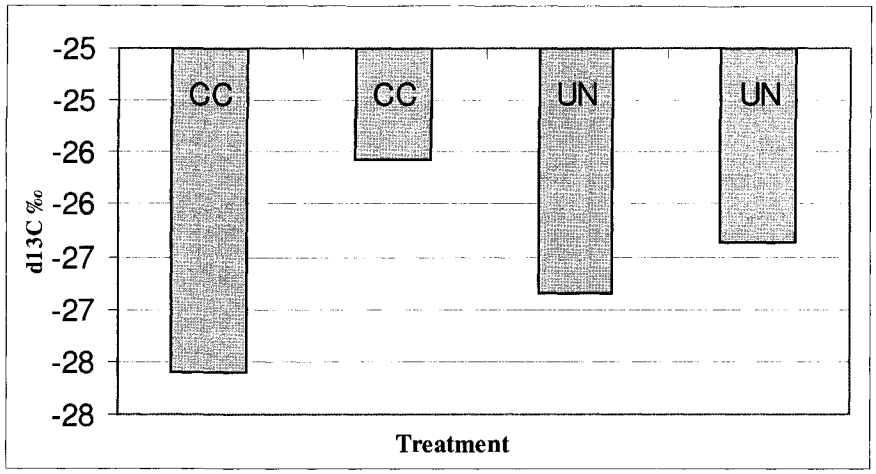


Figure 7.6. SBSmk1, 0-year site $d^{13}C$ values for the cc and un treatments.

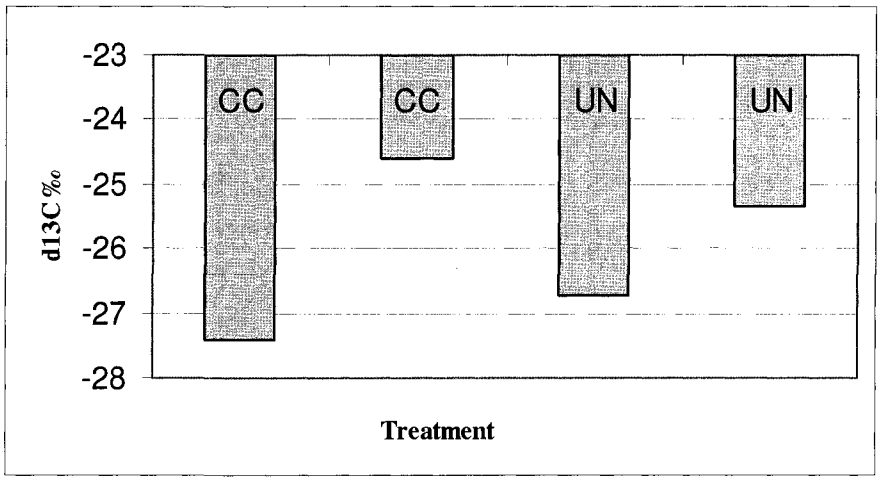
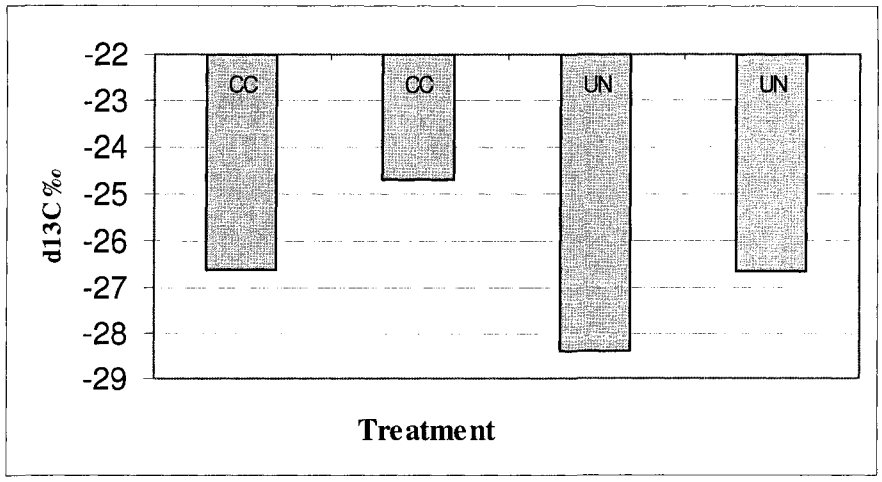


Figure 7.7. SBSmk1, 5-year site $d^{13}C$ values for the cc and un treatments.



8.0 General discussion

8.1 Current status of Douglas-fir single tree retention

The single tree retention system is being applied in the Prince George TSA at a greater rate than in the past because of the unprecedented uplift in allowable annual cut (AAC) due to mountain pine beetle salvage operations. Thus, there is urgency for new information, clarity of current policy and introduction of new policy directed specifically at maintaining mature Douglas-fir stand components. Such policy must be directed at operational (stand level) and strategic planning levels.

In addition to a new insight on how individual leave-trees respond when the surrounding stand is removed, this study has provided critical baseline information addressing a broad range of site and harvesting characteristics in relation to Douglas-fir leave-tree mortality. This study has also highlighted how physiological water stress, and potential post harvest, tree adaptations to such stresses, play a pivotal role in Douglas-fir leave-tree survival or mortality. Other factors such as soil conditions, bark beetles and diseases appear to play a contributing but ultimately secondary role in mortality.

8.2 Research findings

Throughout the Prince George TSA Douglas-fir leave-tree mortality is occurring at variable rates. Water potential, soil water content and temperature, and stable $^{13}C/^{12}C$

ratio values observed in this study suggest the isolated trees in the logged areas were subjected to greater stresses more often than trees in the unlogged areas. It is difficult to tell if trees that have survived postharvest for a number of years have acclimated and will continue to survive. However, there is some evidence that some trees do acclimate to new environments.

It has recently been recognized that high levels of leave-tree mortality in some areas could compromise long term management objectives and the maintenance of forest structure associated with the local disturbance regime (Rogers and Hawkins, 2003). Because many of these tall dominant and veteran trees have low leaf to sapwood area ratios due to self pruning (Philips et al. 2002) and because tree height is important with respect to water relations (Ryan et al. 2000, Phillips et al. 2002, Ryan and Barnard 2003, Koch et al. 2004), trees which have acclimated to the pre harvest environment may be unable to acclimate to the new postharvest environment. A sudden change in water relations is likely a strong contributing factor to mortality of some Douglas-fir leave trees. The change in water relations and effect of the resultant water stress is variable from tree to tree with the potential to be the primary mode of death for some trees and a secondary mode of death for others, predisposing them to attack by bark beetles or fungal pathogens, while other trees appear to compensate and survive.

From this research it is evident that microenvironment (soil and microclimate) characteristics around leave-trees change drastically after the surrounding stand is removed. The potential deleterious effects of some of these changes on the physiology of

these trees are well documented in the literature. Also, Douglas-fir trees that endured the greatest stress most often throughout the growing season were those in the harvested treatment of the recently harvested site, indicating that those trees still surviving in the site harvested 5 years before may have undergone some degree of acclimation.

8.3 Policy and legislation

The importance of the interior Douglas-fir tree species as a landscape attribute has been recognized by the BC Forest Practice Code (FPC) and its Biodiversity Guidebook (1995), BC Ministry of Forests Regional Douglas-fir Management Guidelines (BC Ministry of Forests, 1999) and recent research reviews on the topic (e.g. Lousier and Kessler 1999). In the Chief Forester's Guidance on Landscape and Stand Level Retention (2005), the retention of Douglas-fir in mountain pine beetle salvage areas is emphasized (BC Ministry of Forests, 2005). The latter document states that "where Douglas-fir and other non pine species occur, 'reasonable effort' should be undertaken to retain significant portions of that species at the landscape and cutblock level". As with many government documents, the intent is clear but the language is broad and general. In reality, without some sort of scientifically supported operational guidance such as appropriate retention patch sizes designed to mitigate changes in microenvironment around targeted Douglas-fir retention, terms such as 'reasonable effort' are subjective and can be interpreted and rationalized in ways that have no impact on maximizing stand or landscape level retention success.

As part of the Douglas-fir retention initiative, guidance on landscape and stand level retention must be incorporated into policy and the effectiveness of the policies monitored. Current retention guidelines drafted in a large part to address mountain pine beetle salvage harvesting need to be more explicit regarding retention specifically of Douglas-fir. From the findings of this work, it appears policy regarding mature Douglas-fir retention should state specifically that desired retention trees should be maintained in untouched groups of either pure or mixed species rather than as single trees if maximizing Douglas-fir survival is a primary objective. Conversely, if snag recruitment into future plantations as part of a deadwood cycle is a management objective, higher mortality in single dispersed trees may satisfy this. In order to model the structural contribution of Douglas-fir in future stands in areas where it is highly valued ecologically, current inventories must accurately reflect its spatial distribution both pre and postharvest.

8.4 Barriers to change

Maintaining the distribution of Douglas-fir across the sub-boreal landscape remains a key issue for strategic and operational planners. As previously mentioned, the current mountain pine beetle outbreak has accelerated cutting in pine-fir stands.

The interagency, Licensee Landscape Objective Working Group (LOWG) considered the implementation of biodiversity management in mountain pine beetle impacted landscapes (MSRM, 2004). According to the implementation strategy, licensees will soon be

required to retain "Live old" non-pine species. Licensees are currently using single tree retention systems for large old Douglas-fir. However, if the objective is to maintain levels of "live old" trees then the mortality of these trees soon after harvest creates a barrier to successfully achieving landscape level objectives. A greater mix of single-tree and group retention strategies rather than any single approach would result in structural contributions more closely approximating that of natural disturbances.

Without spatial management by area, the ability to strategically plan and monitor where and how much Douglas-fir is being removed is limited. The economic desirability of Douglas-fir to loggers in some areas has the potential to override its biological value for retention on the landscape. It is not evident that this factor has been incorporated into policy decision making. However, the Prince George LRMP is aware of the issue and is currently exploring the potential impacts of over harvest of Douglas-fir in some areas (Thibeault, Hodges and Beckett, 2006 Pers. Com)[7]. However, the LRMP committee process will likely take time to respond to this issue, and the solution from this process may come after the opportunity to address the retention problem has past (Beckett, 2006 Pers. Com). Currently there is little control over how Douglas-fir is logged. Therefore policy implementation needs to have built in compliance and monitoring.

---

[7] Beckett, D. 2006. BC Ministry of Forests and Range, Timber Supply Analyst, Prince George Region.

[11]Hodges, K. 2006. BC Ministry of Forests and Range, Tenures Forester, Prince George District

[11]Thibeault, R. 2006. Planning Officer, BC Integrated Land Management Bureau Ministry of Agriculture and Lands. Prince George, BC

The "Old forest" definition in the 2005 Biodiversity Order from the provincial government does not consider younger forest with older components. From an inventory prospective this is problematic. The forest inventory is designed to be statistically reliable at a strategic level for a forest management unit, and is not as reliable at a stand level (Beckett, 2006 Pers. Com). As a result, if used as a resource for primary guidance at the stand level, it is a barrier to spatial management of Douglas-fir. For this reason, it is necessary to ground truth strategic planning efforts and update forest inventories to ensure that retention is effective at meeting stand and landscape level objectives.

A further consideration in long-term stand-level and landscape planning is the potential impact of future climate change. For example, on Vancouver Island Hebda (1997), using relative abundance of costal western hemlock *Tsuga heterophylla* (Raf.) Sarg pollen found on lake beds in relation to Douglas-fir pollen found that under dryer warmer historical climatic conditions, Douglas-fir once dominated where hemlock now dominates. This demonstrates the effect that climate change can have on species that are sensitive to environmental changes. Current work in BC to examine the sensitivity of interior Douglas-fir to climate change has just begun (FGC, 2006, Greisbauer and Green, 2006[8]). The Ministry of Forests and Range through progeny testing, tree breeding and seed conservation for interior Douglas-fir of geographically unique seed planning units has suggested that if projected climate change occurs, genetic stock from more southerly,

[8] Greisbauer, H. and Green, S. 2006. Predicting the response of interior Douglas-fir to climate change in BC University of Northern British Columbia.

drier ecosystems may have better growth and survival potential when planted in more northerly geographic locations.

8.5 Operational Recommendations

Regulatory agencies, forest licensees, and the general forestry community recognize the importance of residual Douglas-fir at both stand and landscape levels but they do not appear to have all the information required to appreciate the complexities of achieving these objectives 'on the ground'. This research addresses some of the complexities and provides operational recommendations intended to maximize the success of retention strategies around Douglas-fir.

Long-term landscape level management strategies should include promotion of Douglas-fir regeneration by planting, and also include the maintenance of larger trees to meet long term biodiversity, and immediate habitat structural objectives. However, a greater emphasis is recommended for leaving untouched patches (clumps) with trees from multi cohorts and in general applying a range of retention approaches. Thus, due to the change in microenvironment surrounding Douglas-fir trees after harvesting, it is emphasized that group retention strategies be included more often as planning options.

Although planting Douglas-fir addresses some long term goals, it does not address the preservation of existing forest structure or the longevity of large old Douglas-fir trees that contribute to natural regeneration and wildlife habitat. In order for regional objectives to

be realized, the ecological processes and factors affecting survival rates of Douglas-fir leave-trees must be further investigated, and the resulting recommendations conveyed to forest managers.

8.6 Research recommendations

In the recent BC government Biodiversity Order (BC Provincial Government, 2005), it is stated that once there is new information available to verify landscape condition and the extent of mountain pine beetle impact is fully realized, the interim measure for natural forest areas, to ensure species representation will be revisited (BC Provincial Government, 2005). Thus, in light of the inherent connection between Douglas-fir in central BC and mountain pine beetle infested stands, empirical data for Douglas-fir response to harvesting from numerous operational retention scenarios should be conducted in order to determine retention success rates.

Due to the high variability in stress response found among trees in this study, future work at this level should focus on pre and postharvest changes around individual sample trees rather than using trees adjacent to a cutblock as controls. Therefore, repeated measure sampling of individual trees before and after logging would give a more precise measure of Douglas-fir leave-tree response to harvesting under a variety of retention treatments. This would eliminate a major source of uncontrolled statistical variation from site factors. In order to effectively make reliable quantitative projections about the survivorship of leave-trees, larger scale block age versus standing mortality surveys need to be conducted

to calculate mortality rates of leave-trees over longer periods of time than was used in this study.

If leave-trees are to be left in clumps within patches, the dynamics of spatial gradients in relation to edge and their proximal effects on inner trees needs to be explored in order to effectively design retention patch sizes that optimize leave-tree survivorship while addressing economic requirements. Study designs using water potential and stable isotope ratios to determine water stress could then incorporate a variety of operational scenarios including variable patch sizes.

Although it is recognized that ultimately climate change may result in greater forest productivity or conversely may exacerbate forest health problems it is not known what the immediate effects on individual tree species will be (BCMoFR, 2006). Therefore, long-term studies that address Douglas-fir sensitivity to climate change coupled with a range of silviculture systems should be established.

8.7 Conclusion

As a retention silviculture system, the Douglas-fir single leave-tree retention currently being carried out by forest licensees in central BC is a positive step toward meeting long term landscape level biodiversity objectives but its effectiveness is limited if unexpected mortality occurs. The intent is that live Douglas-fir be retained to provide more diverse structure and natural species composition in future plantations. This silviculture

approach acknowledges that the conservation of this species is essential to the maintenance of unique forest structure and habitat quality of the central interior. However, further knowledge as to the extent and success of current retention under the present guidelines is needed.

In order to accommodate mountain pine beetle salvage strategies, cumulative areas harvested continue to increase substantially in areas of Central BC where much of the Douglas-fir occurs as secondary and tertiary stand components. The result is an even greater number of cutblocks with single Douglas-fir leave-trees. Consequently there is an immediate need to explore new and functional operational retention strategies and ensure there is legislative policy to guide and implement them at both the strategic and operational levels.

Having a broader temporal and spatial understanding of mortality at stand and landscape levels will aid planners, modelers and policy makers in developing new Douglas-fir retention guidelines and more effective operational retention methods to increase stand level retention survival. Operational adjustment factors (OAF) that incorporate projected leave-tree mortality/survival into modeled mortality functions can then be developed and incorporated into timber supply analysis models.

There needs to be refinement of policy that deals with harvesting and retention practices of Douglas-fir in Central BC. Strategic planning for successful long term retention of live Douglas-fir must become part of strategic mountain pine beetle salvage planning

operations. Considering that the reliability of the forest cover inventory is limited at the stand level, operational planning needs to be driven by spatial rather than aspatial strategic objectives in order to focus management appropriately at the stand level rather than managing strictly by volume. In order to achieve this, a better understanding of how to optimize the survival of retained leave-trees is also required. If these strategic and operational needs are not met, increased harvest and single tree retention of Douglas-fir in sensitive habitat management areas will continue. This will result in increases in mortality of retained Douglas-fir trees, decreases in habitat quality, and decreases in the genetic potential of natural Douglas-fir at this latitude.

It appears that some leave-trees acclimate to increased water stress with time since harvest. A better understanding of how this is achieved will aid planners in attaining desired outcomes. With a better understanding of how to successfully retain mature Douglas-fir and an accurate knowledge of its abundance and distribution, more positive long-term management outcomes will be realized.

Literature Cited:

Acker S. A., C. B. Halpern, M. E. Harmon, and C. T. Dyrness. 2002. Trends in bole biomass accumulation, net primary production and tree mortality in *Pseudotsuga menzisii* forests of contrasting age. Tree Physiol. 22:213-217.

Adams, P.W., Flint, A.L., and R.L. Fredrikson, 1991. Long-term patterns in soil moisture and revegetation after a clearcut of a Douglas-fir forest in Oregon. For. Ecol. Manage. 41:249-263.

Alder, N.N., J.S. Sperry and W.T. Pockman. 1996. Root and xylem embolism, stomatal conductance, and leaf turgor in *Acer grandidentatum* populations along a soil moisture gradient. Oecologia 105:293-301. (Cited in: Stout and Sala, 2003).

Anonymous, 2006. Preparing for climate change: adapting to impacts on British Columbia's forest and range resources. BC Ministry of Forests and Range pp. 25-26.

Arndt, S.K., and W. Wanek, 2003. Use of decreasing foliar carbon isotope discrimination during water limitation as a carbon tracer to study whole plant carbon allocation. Plant Cell Environ. 25:609-616.

Barnard, H.R. and M.G. Ryan, 2003. A test of the hydraulic limitation hypothesis in fast growing *Eucalyptus saligna.* Plant Cell Environ. 26:1235-1245.

Bassuk, N. and T. Whitlow. 1986. Urban stress is not limited to people . American Nurseryman, pp. 57-61.

Bauerle, W. L., Hinckley, J., and Kucera, J., 1999. The canopy water relations of old-growth Douglas-fir trees. Trees, Vol 13: 211-217.

BC Ministry of Forests, 1999. Forest Practice Code Note No. 2. Douglas-fir Management Guidelines for the Prince George Forest Region. Victoria, BC.

BC Ministry of Forests, 1995. Biodiversity Guidebook. Forest Practices Code of British Columbia Act, Strategic Planning Regulations, Operational Planning Regulation. Victoria, BC.

BC Ministry of Forests, 2004. Minister's response to the Forest and Range Practices Advisory Council (On draft regulations and RFPA implementation). pp 11-14. http://www.for.gov.bc.ca/code/pac/PAC_Response_final.pdf (accessed June 10, 2006)

BC Ministry of Forests, 2005. Review prepared by K. Hodges. Chief Forester's guidance on landscape and stand level retention. For large-scale mountain pine beetle salvage harvesting operations. Prince George Forest District, Requested operational lens review.

BC Provincial Government, 2002. Backgrounder report. A Results-based forest practices regime for British Columbia. British Columbia Provincial Government, Victoria, BC pp. 3.

BC Provincial Government, 2005. Order establishing landscape level biodiversity objectives for the Prince George Timber Supply Area. BC Provincial Government. pp 5-7.

Becker, P., F.C., Meinzer, and S.D. Wullschleger, 2000. Forum comment on 'Hydraulic limitation of tree height. Functional Ecology 14:135-140.

Bender, M.M. and A.J. Berge. 1982. Carbon isotope records in Wisconsin trees. Tellus 34:500-504.

Bladon, K.D., U. Silins, S.M. Landhausser and V.J. Lieffers, 2005. Differential transpiration by three boreal tree species in response to increased evaporative demand after variable retention harvesting. Agriculture and Forest Methodology 138:104-119.

Bodapti, P, D. Aspinall and L.G. Paleg, 1992. Variability in proline-accumulating ability of barley (*herdum vulgare* L.) cultivars induced by vapor pressure deficit. Plant Physiol. 98:716-722.

Boggess, S.F., D. Aspinall, L.G. Paleg, 1976. Stress metabolism. IX. The significance of end-product inhibition of proline biosynthesis and of compartmentation in relation to stress-induced proline accumulation. Aust. J. Plant Physiol. 3: 513-525.

Bond, B.J. and Kavanagh, K.L. 1999. Stomatal behavior of four woody species in relation to leaf specific hydraulic conductance and threshold water potential. Tree Physiology: 19, 503-510.

Bond, B. J., M.G. Ryan and M. Williams, 1999. Stand age, productivity and hydrologic conductance of Douglas-fir in the Wind River Basin. Oregon State University, U.S. Forest Service, Woods Hole Marine Biological Laboratory.

Bowling, D.R., N.G. McDowell, B.J. Bond, B.E. Law and J.R. Ehleringer, 2002. ^{13}C content of ecosystem respiration is linked to precipitation and vapor pressure deficit. Oceologia. 131: 113-124.

Brade, B. 2003. Mule Deer Ungulate Winter Range Proposal. Forest Ecosystem Biologist, Omineca Region, British Columbia Ministry of Water, Land and Air Protection.

Brady, N.C. 1990. The nature and properties of soils. Tenth Addition. Macmillan Publishing Company, New York, pp. 403.

Brooks, J.R., L.B. Flanagan, G.T. Varney and J.R. Ehleringer, 1997. Vertical gradients in photosynthetic gas exchange characteristics and refixationof respired CO_2 within boreal forest canopies. Tree Physiology 17:1-12. Cited in Cregg and Zahng, 2000.

Bucci, S.J., F. J. Scholz, G. Goldstein, F.C. Meinzer, J.A. Hinojosa, W.A. Hoffman and A.C. Franco, 2004. Processes preventing nocturnal equilibrium between leaf and soil water potential in tropical savanna woody species. Tree Physiology. 24:1119-1127.

Burns, B., Gallus, J. and Martin, K., 2003. A study of Plants Reaction to Water Stress and Available Moisture, FOR 332, The University of Massachusetts Press: Massachusetts.

Burton, Philip J. 2002. Effects of clearcut edges on trees in the sub-boreal spruce zone of Northwest-central British Columbia. Silva Fennica 36: 329-352.

Cleary, B.D. and Zaerr, J.B. 1980. Pressure Chamber Techniques for monitoring and evaluating seedling water status. N.Z.,J.F.S. 10: 133-141.

Clark, J.R. and R. Kjelgren. 1989. Conceptual and management considerations for the development of urban tree plantings. J. Arboric. 15:229-236.

Chappelka A.H. and Samuelson L.J. 1998. Ambient ozone effects on forest trees of the eastern United States: a review. New Phytol 139:91–108. (Cited in: Bauerle et al. 1999).

Coder, K.D. 2000 (last updated). Soil compaction impacts on tree roots. University of Georgia, extension publication FOR00-8. http://www.ag.iastate.edu/departments/forestry/ext/roadside_tree_management/for00-003.pdf

Comstock, J.P. 2002. Hydraulic and chemical signaling in the control of stomatal conductance and transpiration. J.Exp.Bot. 53: 195-200.

Coombs, J., Hall, D.O., Long, S.P., Scurlock, J.M.O. 1985. Techniques in Bioproductivity and Photosynthesis, Second Edition. Pergamon Press ,Oxford, pp 298.

Cowan, I. R., 1994. As to the mode of action of guard cells in dry air. Ecophysiology of Photosynthesis, edited by E.D. Schulze and M.M. Caldwell, pp 205-209, Springer – Verlag, New York.

Craig, H. 1957. Isotopic standards for carbon and oxygen and correlation factors for mass-spectrometric analysis of carbon dioxide. Geochim. Acta 12:133-149.

Cregg, B.M. and Zhang, J. 2000. Carbon isotope discrimination as a tool to screen for improved drought tolerance. Proceedings of the 11th conference of the Metropolitin Tree Improvement Aliance held in conjunction with the Lanscape Plant Development Centre. Gresham OR.

Cregg, B.M. 1994. Carbon allocation, gas exchange, and needle morphology of *Pinus ponderosa* genotypes known to differ in growth and survival under imposed drought. Tree Physiol. 14:883-898

Crombie, D.S., M.F. Hipkins and J.A. Milburn. 1985. Gas exchange penetration of pit membranes in the xylem of Rhododendron as the cause of acoustically detectible xylem cavitation. Aust. J. Plant Physiol. 12:445-453.

Decoteau, D.R., 2005. Principles of Plant Science. Person Education Inc., Upper Saddler River, New Jersey 07458. pp 91-92 and pp 296.

DeLong, S.C. 1999. Ecology of Douglas-fir at its Northern Limits (Cited in: Lousier, J.D. and Kessler, W.B., 1999 pp 27-38).

Delong S.C. 2003. A Field Guide to Site -Identification and Interpretation for the Southwest Portion of the Prince George Forest Region. Land Management Handbook 24, BC Ministry of Forests. http://www.for.gov.bc.ca/hfd/pubs/Docs/Lmh/Lmh24.htm (accessed June 9, 2006)

Dingman S.L., 1994. Physical hydrology. New York : Macmillan Pub. Co.; Toronto : Maxwell Macmillan Canada ; New York : Maxwell Macmillan International.

Donovan, L.A., D.J.Grise, J.B. West, R.A. Pappert, N.N. Alser and J.H. Richards, 1999. Predawn disequilibrium between plant and soil water potentials in two cold-desert shrubs. Oecologia. 120:209-217.

Donovan, L.A., M.J. Linton and J.H. Richards, 2001. Predawn plant water potential does not necessarily equilibrate with soil water potential under well watered conditions. Oecologia. 129:328-335.

Doucett, R. 2004 (last updated). Colorado Plateau Stable Isotope Laboratory Web Page. http://www4.nau.edu/cpsil/ (accessed June 9, 2006).

Duniway, J.M. 1971. Comparison of Pressure Chamber and thermocouple psychrometer determinations of leaf water status in tomato. Plant Physiol. 48:106-107.

Ehleringer, J.R., A.E. Hall and D.D. Farquhar, 1993. Stable isotopes and plant carbon/water relations. Academic Press, San Diego.

Farrar, J.L. 1995. Trees in Canada. Her majesty the Queen in Right of Canada, ISBN 1-55041-199-3, Cat. No. Fo42-234/1995E.

Farquhar, G.D. and R.A. Richards. 1984. Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. Aust. J. Plant Physiol. 11:539-552.

Farquhar, G.D., J.R. Ehleringer and K.T. Hunick, 1989. Carbon isotope discrimination and photosynthesis. Annu Rev Plant Physiol Plant Mol Biol 40: 503-537.

Fischer, D.G., T.E., KolB and L.E. Dewald, 2002. Changes in whole-tree water relations during ontogeny of *Pinus Flexis* and *Pinus ponderosa* in a high-elevation meadow. Tree Physiology. 22:675-685.

FGC, 2006. The Forest Genetics Council of British Columbia. http://www.fgcouncil.bc.ca/ (updated 2006 and accessed December 2006).

Franklin, J.F. and C.B. Halpern. 2000. Pacific Northwest forests. In: North American terrestrial vegitaion. 2nd Edn. Eds. M.G. Barbour and W.D. Billings. Cambridge University Press, New York, pp 123-159.

Frederickson T.S., Skelly JM, Steiner K.C., Kolb T.E., Kouterick K.B.1996) Size-mediated foliar response to ozone in black cherry trees. Environ. Pollut. 91:53–63. (Cited in: Bauerle et al. 1999).

Fuhrer, E. 1988. Oak decline in central Europe: A synopsis of hypotheses. Proceedings: Population dynamics, Impacts, and Integrated Management of Defoliating Insects. USDA For. Ser. GTR NE-247. pp 18.

Gao, Q., Zhao, P., Zeng, X., Caf, X. and Shen, W. 2002. A model of stomatal conductance to quantify the relationship between leaf transpiration, microclimate and soil water stress. Plant, Cell Environ., 25:1373-1381.

Garcia-G, R., A. Gome, J. Lopez-U, J. Vargas-H and W.R. Horwath. 2004. Tree Gorowth and $d^{13}C$ among populations of *Pinus greggii* Engelm. At two contrasting sites in central Mexico. Forest Ecology and Management 198: 237 – 247.

Gliexner, G., H.J. Danier, R.A. Werner and H.L. Schmidt. 1993. Correlations between the ^{13}C content of primary and secondary plant products in different cell compartments and that in decomposing basidiomycetes. Plant Physiol. 102:1287-1290.

Gliexner, G., C. Scrimgeour, H.L. Schmidt and R. Vola, 1998. Stable isotope distribution in the major metabolites of source and sink organs of *Solanum tuberosum* L.: a powerful tool in the study of metabolic partitioning in intact plants. Planta 207:241-245.

Grier, C.C., K.M. Lee, N.M. Nadkarni, G.O. Klock and P.J. Edgerton, 1989. Productivity of forests of the United States and its relation to soil and site factors and management practices: a review. USDA, For. Serv. GTR. PNW-222, 51p. (Cited in: Acker et al. 2002).

Grifiths, R. P. and A.K. Swanson, 2000. Forest soil Characteristics in a chronosequence of harvested Douglas-fir forests. Can. J. For. Res. 31:1871 – 1879.

Grulke N.E. and P.R Miller. 1994. Gas exchange characteristics from seedlings to mature trees in giant sequoia: implications for response to current and future concentrations of atmospheric ozone. Tree Physiol. 14:659–668.

Guy, R.D. and D.L. Holowachuk. 2001. Population Differences in stable carbon isotope ratio of *Pinus contorta* Dougl. Ex Loud.: relationship to environment, climate of origin, and growth potential. Can. J. Bot. 79:274-283.

Halmschlager, E. 1997. Die Rolle von *Armillaria* spp. und *Phytophthora* spp. Im Krankheitssyndrom der Eichen. Vorläufige Ergebnisse einer dreijährigen Untersuchung in zwei erkrankten Eichenbeständen in Ostösterreich. Znanje za gozd. Zbornik 50:1997: 233-244. (Cited in Fuhrer, 1988).

Hanson, E.M. and K. J. Lewis, (edited by) 1997. Compendium of Conifer Diseases. The American Phytopathological Society, 3340 Pilot Knob Road, St. Paul, MN.

Hartmann, G. 1996 Ursachenanalyse des „Eichensterbens" in Deutschland Versuch einer Synthese bisheriger Befunde. In: Wulf and Kehr (eds.): Mitt. Biol. Bundesanst. Land u. Forstw. Berlin, H 318: 125-151. (In:Fuhrer, 1988).

Hebda, R. 1997. Atmospheric change, forests and biodiversity. Botany and Earth History, Royal British Columbia Museum Victoria, BC, V8V 1X4, Canada and Biology and School of Earth and Ocean Sciences, University of Victoria, PO Box 1700, Victoria, British Columbia, V8W 2Y2, Canada.

Hemming, D., H. Fritts, S.W. Leavitt, W. Wright, A. Long and A. Shashkin. 2001. Modeling tree ring $d^{13}C$. Dendrochronologia 19:23-38.

Hendrick, R.L. and K.S. Pregitzer, 1993. The dynamics of fine root length, biomass and nitrogen content in two northern hardwood ecosystems. Canadian Journal of Forestry Research 23:2507-2520.

Henigman, J., Ebata, T., Allan, E., Westfall, J., Pollard, A. 2001. Field Guide to Forest Damage in British Columbia. Joint publication between the governments of Canada and British Columbia, ISSN 0843-4719 ; no. 17.

Hepting, G. H. 1971. Diseases of forest and shade trees of the United States. U.S. Department of Agriculture, Agriculture Handbook 386. Washington, DC. 658 p. *In*; Herman and Lavender, 1988.

Herkelrath 1991 Automatic, real-time monitoring of soil moisture in a remote field area with time domain reflectometry Water. Resour. Res. 27: 857-864.

Hermann, R. K. 1985. The genus Pseudotsuga: Ancestral history and past distribution. Oregon State University, College of Forestry, Forest Research Laboratory Special Publication 2b. Corvallis. pp 32.

Hermann, R.K. and D.P., Lavender, 1988. Douglas-fir. Silvics of North America, V- 1. United States Department of Agriculture, Forest Service. Agriculture Handbook 654. pp 10.

Hinckley, T.M., J.P. Lassoie, and S.W. Running, 1978. Temporal and spatial variations in water status of forest trees. For Sci Monogr 20. (Cited in: Donovan et al. 2001).

Hinkley T. M. and J.H. Braatne, 1994. Stomata, in Plant and Environment Interactions, edited by R.E. Wilkinson, Marcel Decker, New York 99:323 – 355.

Hook and Livingston 1996. Errors in converting time domain reflectometry measurements of propagation velocity to estimates of soil water content. Soil Science Society of America Journal 60: 35-41.

Houston, D. R. 1990. In: Manion, P.D. and Lachance D. 1992. Forest Decline Concepts. A host stress saprogen model for forest die-back decline diseases. The American Phytopathological Society. Library of Congress Cat. No.: 92-73742. pp 5.

Huang, J., S.T. Lacey and P. J. Ryan, 1996. Impacts of forest harvesting on the hydraulic properties of surface soil. Soil Science, Vol. 161, No. 2. pp 79.

IUFRO, 2002. Forests and Water: Relations between Forest Ecosystems and Water Resources. International Union of Forest Research Orginizations. http://iufro.boku.ac.at/iufro/. August-September, 2002.

Jackson, M.B. 2002. Long-distance signaling from roots to shoots assessed : the flooding story. J. Exp. Bot., 53:175-181.

Jaggi, M., M. Saurer, J. Fuhrer and R. Siegwolf. 2002. The relationship between the stable carbon isotope composition of needle bulk material, starch, and tree rings in *Picea abies.* Oecologia 131:325-332.

Jalkanen, R., 1997. Abiotic Diseases. In: Hanson and Lewis, 1997. pp 64.

Johnson, R. 1992. Elementary Statistics, Sixth Edition. Library of Congress Cataloging-in-Publication Data, ISBN 0-534-92980-x, pp. 534.

Jones, H. and R. Sutherland. 1991. Stomatal control of xylem embolism. Plant Cell Environ. 17:607-612. In Bond and Kavanagh, 1999. pp. 508.

Jones, H.G. 1992. Plants and microclimate, 2nd edition. Cambridge University Press, Cambridge.

Jones, M.D., D.M Durall,.M. Harniman, D. C. Classen, and S. W. Simard. 1988. Ectomycorrhizal Diversity of Paper Birch and Douglas-fir Seedlings Grown in Single-species and Mixed Plots in the ICH Zone of Southern British Columbia. BC Ministry of Forests, Forest Science Program, Extension Note #19.

Jull, M., 1999. Douglas-fir Silviculture "on the Edge", Silvicultural Systems at the Northern Limit of the Species. (Cited in: Lousier, J.D. and Kessler, W.B., 1999 pp 34-44).

Kanaskie, A., D. Overhulser, and M. McWilliams, 1999. Forest Health in Oregon, 1999 (Mortality and dieback of Douglas-fir from water stress). The Oregon Department of Forestry, in cooperation with the U. S. Forest Service.

Kaufman, M.R. 1968. Evaluation of the pressure chamber technique for estimating plant water potential in Forest Tree Species. For. Sci.. 14:369-374.

Kavanagh, K.L., and J. Zaerr, 1997. Xylem cavitation and loss of conductance in western hemlock following planting. Tree Physiol.17:59-63.

Kelly J.M., L. Samuelson, G. Edwards, P. Hanson , D. Kelting, A. Mays, S. Wullschleger, 1995. Are seedlings reasonable surrogates for trees? An analysis of ozone impacts on *Quercus rubra*. Water, Air Soil Pollut 85:1317–1324. (Cited in: Bauerle et al. 1999).

Kemp L. and R. Shuller 1982. Checklist of the vascular plants of Thorton T. Munger Research Natural Area. USDA Forest Ser-vice PNW-4, February 1982. In: Bauerle et al. 1999.

Klinka, K., J. Worrall, L. Skoda and P.Varga. 2000. The Distribution and Synopsis of Ecological and Silvicultural Characteristics of Tree Species of British Columbia's Forests. Canadian Cartograhics Ltd., Coquitlam, BC.

Koch G.W., Sillett, S.C., Jennings, G.M. and Davis, S.D. 2004. The limits to tree height. Nature 428:851-854.

Körner C, G.D. Farquhar and Z. Roksandic, 1988. A global survey of carbon isotope discrimination in plants from high altitude. Oecologia 74: 623–632.

Kozlowski, T.T. and S.G. Pallardy, 1997. Physiology of woody plants, 2nd edition. Academic Press, San Diego.

Lanner, R. M. 1961. Living stumps in the Sierra Nevada. Ecology 42:170-173.

Latham P. and J. Tappeiner. 2002. Response of old growth conifers to reduction in stand density in western Oregon forests. Tree Physiology, 22:137-146.

Leavitt, S.W. and A. Long. 1982. Evidence for $^{13}C/^{12}C$ fractionation between tree leaves and wood. Nature. 298: 742-744.

Leavitt, S.W. and A. Long. 1986. Stable carbon isotope variability in tree foliage and wood. Ecology. 67:1002-1010.

Leavitt S.W. and S.R. Danzer, 1993. Methods for batch processing small wood samples to holocellulose for stable-carbon isotope analysis. Analytical Chemistry. 65:87-89.

Le Roux-Swarthout, D. V. Terwilliger, M., Christianson, C. Martin and S. Madhaven, 2000. Carbon isotope discrimination correlates with a range of ratios of photoenol pyruvate to carboxylase activities found in two C_3 species. J. Plant Physiol. 157: 489-493.

Livingston N.J. and D.L. Spittlehouse, 1996. Carbon isotope fractionation in tree ring early and late wood in relation to intra season water balance. Plant, Cell and Environment. 19:768-774.

Lewis, K.J. and E.M. Hanson. 1991. Survival of *Inonotus tomentosus* in stumps and subsequent infection of young stands in north central British Columbia. Can. J. For. Res. 21:1049-1057.

Lousier, J.D. and Kessler, W.B., 1999. Proceedings of a workshop on The Ecology and Management of Northern Interior Douglas fir. University of Northern British Columbia and BC Ministry of Forests, Prince George. pp 34-44 and 29-33.

LRMP, 2004. Regional Land Use Plans and Land Resource Management Plans (LRMPs) in British Columbia (http://srmwww.gov.bc.ca/rmd/lrmp/), accessed March 2004.

Lu, Z. and Neumann, P.M. 1999. Water stress inhibits hydraulic conductance and leaf growth in rice seedlings but not the transport of water via mercury-sensitive water channels in the root. Plant Physiol. 120:143–152.

Madhavan, S., I. Treichel and M.H. O'Leary, 1991. Effects of relative humidity on carbon isotope fractionation in plants. Bot Acta 104: 292–294.

Magnani, F., M. Mencuccini, and J. Grace, 2000. Age-related decline in stand Productivity: the role of structural acclimation under hydraulic constraints. Plant Cell Environ. 23:251-263.

Manion, P.D., 1997. Decline Deseases. In: Hanson and Lewis, 1997. pp67.

Martin, C.W., J.W. Hornbeck, G.E. Likens, and D.C. Buso. 2000. Impacts of intensive harvesting on hydrology and nutrient dynamics of northern hardwood forests. Can. J. For. Res 57:19-29.

McDowell, N., H. Barnard, B. J. Bond, T. Hinckly, R.M. Hubbard, H. Ishii, B. Kostner, F. Magnani, J.D. Marshal, F.C. Meinzer, N. Phillips, M.G. Ryan and D. Whitehead, 2002a. The relationship between tree height and leaf area:sapwood ratio. Oceologia 132:12 20.

McDowell N., N. Phillips, C. Lunch, B.J. Bond and M.G. Ryan, 2002b. An investigation of hydraulic limitation in large old Douglas-fir trees. Tree Physiol. 22:763-744.

McDowell N., J.R. Brooks, S.A. Fitzgerald and B.J. Bond, 2003. Carbon isotope discrimination and growth response of old Pinus Ponderosa.

McDowell, N., D.R. Bowling, B.J. Bond, J. Irvine, B. Law, P. Anthony, J. Ehleringer, 2004. Response of the carbon isotopic content of ecosystem, leaf, soil respiration to meteorologivcal physiological driving factors in a *Pinus ponderosa* ecosystem. Global Biogeochemical cycles. 18:1013-1029.

Meinzer, F.C. 2003. Functional convergence in plant response to the environment. Oecologia, 134:1-11.

Ministry of Forests, 2002. Pothole Creek Study - Tree Physiology and Moisture Relations. Forestry Division Services Branch, Victoria, BC.

Ministry of Forests, 1998. Site index estimates by site series for coniferous tree species in British Columbia. Forestry Division Services Branch, Victoria, BC.

Montieth, J.L. 1995. A reinterpretation of stomatal responses to humidity. Plant Cell Environ., 18: 357 – 364.

MSRM, 2004. Landscape Objective Working Group. Background information and supporting documentation for the development of the Prince George timber supply area, landscape level biodiversity objectives. Ministry of Sustainable Resource Management, Northern Interior Prince George Region. pp. 16-19 and pp. 24.

Myren, D.T and R.F. Patton, 1971. Establishment and spread of Polyporus tomentosus in pine and spruce plantations in Wisconsin. Can. J. Bot. 49:1033-1040. In: Lewis, 1991.

Nippert, J.B. and J.D. Marshal. 2003. Sources of variation in ecophysiological parameters in Douglas-fir and Grand-fir canopies. Tree Physiology. 23:591-601.

Oren, R.J., J.S. Sperry, G.G. Katul, D. E. Pataki, B.E. Ewers, N. Phillips and K.V.R. Schafer, 1999. survey and synthesis of intra- and inter-specific variation in stomatal sensitivity to vapor pressure deficit, Plant Cell Environ., 22: 1515 – 1526.

Passioura, J. B. 2002. Soil conditions and plant growth. Plant, Cell Environ. 25:311-318.

Pederson, B.S. 1988. The role of stress in the mortality of Midwestern oaks as indicated by growth prior to death. Ecology. 79:79–93.

Philips, N., Bond, B J., McDowell, N. G. and Ryan, M. G. 2002. Canopy and hydraulic conductance in young, mature and old Douglas-fir trees. Tree Physiol. 22:205-211.

Philips, N., Bond, B J., McDowell, N. G., Ryan, M. G. and A. Schauer, 2003. Leaf area compounds height-related costs of water transport in Oregon White Oak trees. Functional Ecology 17:832-840.

Prat, W.P. and Schnelle, M.A. 2003 (up date). Site disturbance and tree decline. Oklahoma State University, Extension Fact Sheet F-6429, Stillwater, Oklahoma, USA.

Pregitzer, K.S. M.E. Kubiske, C.K. Yu and R.L. Hendrick, 1997. relationships among root branch order, carbon and nitrogen in four temperate species. Ocologia 111:302-308.

Proulx, G. and Yaremko, L. 2004. A proposal for "Surveys of tracks of mule deer, other ungulates, and furbearers within proposed ungulate winter ranges in the Prince George and Vanderhoof Forest Districts. Alpha Wildlife Research and Management Ltd, Sherwood AB.

Prpic, B. and D. Raus. 1987. Stieleichensterben in Kroatien im Licht ökologischer und vegetations-kundlicher Untersuchungen. Österr. Forstz. 98: 55-57. (Cited in: Fuhrer, 1988).

Raven, P.H., R.F. Evert, S.E. Eichhorn, 1992. Biology of Plants 5th Edition. Library of Congress Catalog Number: 91-72015.

Ritchie, G.A. and Hinckley, T.M. 1975. The Pressure Chamber as an Instrument for Ecological Research. Advanc. Ecol. Res. 9:165-254.

Redfern, Derek B. 1991. Climatic injury as a problem of introduced species in northern Britain. Forestry Commission, Northern Research Station, Roslin, Midlothian, EH25 9SY, UK. Edited by Jalkanen, Risto, Tarmo Aalto, and Marja-Lea Lahti for Forest Pathological Research in Northern Forests with a Special Reference to Abiotic Stress Factors. Extended SNS meeting in forest pathology in Lapland, Finland, August 3-7. 1992.

Rhodes D., S. Handa, 1989. Amino acid metabolism in relation to osmotic adjustment in plant cells. In "Environmental Stress in Plants: Biochemical and Physiological Mechanisms", NATO ASI Series, Vol. G19 (JH Cherry ed), Springer, Berlin, pp. 41-62.

Rhodes D., S. Handa, R.A. Bressan, 1986. Metabolic changes associated with adaptation of plant cells to water stress. Plant Physiol. 82: 890-903.

Richter, H. 1997. Water relations of plants in the field: some comments on the measurement of selected parameters. J Exp Bot. 48:1-7.

Ritchie, G.A. and T.M. Hinckley, 1975. The pressure chamber as an instrument for ecological research. Adv Ecol Res. 9:165-254. (Cited in: Donovan et al. 2001).

Rogers, B.J. and C.D. Hawkins, 2003. Douglas-fir leave-tree mortality; implications for biodiversity and policy. In: proceedings 4th North American Forest Ecology Workshop, Corvallis Oregon (Abstract).

Ryan, M. G. and B. J. Yoder. 1997. Hydraulic limits to tree height and tree growth. Bioscience. 47:235-242.

Ryan, M.G., D. Binkley and J.H. Fownes. 1997. Age-related decline in forest productivity: pattern and process. Adv. Ecol. Res. 27: 213-262. (Cited in: Acker et al. 2002).

Ryan, M.G, B.J. Bond, B.E. Law, R.M. Hubbard, D. Woodruff, E. Clenciala and J. Kucera, 2000. Transpiration and whole tree conductance in ponderosa pine trees of different heights. Oecologia 124:533-560.

Sala, A., E.V. Carey, and R.M. Callaway, 2001. Dwarf mistletoe affects whole-tree water relations of Douglas-fir and Western larch primarily through changes in leaf to sapwood ratios. Oecologia 126:42-52.

Salsbury, F. and Ross, C.W. 1978. Plant physiology (second edition). Wadsworth Publishing Company INC. Library of Congress Cataloging in Publication Data. QK711.2S23-1978. pp. 389, pp. 57-62 and pp. 365. (Cited in: Herman and Lavender, 1988)

Santantonio, D., and R. K. Hermann. 1985. Standing crop, production, and turnover of fine roots on dry, moderate, and wet sites of mature Douglas-fir in western Oregon. Annales des Sciences Forestieres 42(2):113-142.

Samuelson L.J. and G.S. Edwards, 1993. A comparison of sensitivity to ozone in seedlings and trees of *Quercus rubra* L. New Phytol 125:373–379. (Cited in: Bauerle et al. 1999).

Schleser, G.H. 1992. $d^{13}C$ pattern in a forest tree as an indicator of carbon transfer in trees. Ecology 73:1922-1925.

Schulze, B., C. Wirth, P. Linke, W.A. Brand, I. Kuhlmann, V. Horna and E. Schulze. 2004. Laser ablation – combustion – GC – IRMS – anew method for online anlysis of intra-annual variation of $d^{13}C$ in tree rings.

Simpson, D.G. 2000. Water use of interior Douglas-fir. Can. J. For. Res. 30:534-547.

Schmitz, R.F. and K.E Gibson, 1996. Douglas-fir beetle. USDA Forest Service Forest Insect and Disease Leaflet 5. 7 p.

Sperry, J.S and M.T. Tyree, 1990. Water stress induced xylem embolism in three species of conifers. Plant Cell Environ. 13:427-426.

Sperry, J.S., N.N. Alder, and S.E. Eastlack, 1993. The effect of reduced hydraulic conductance on stomatal conductance and xylem cavitation. Journal of Experimental Botany 44:1075-1082.

Sperry, J. S and W.T. Pockman, 1993. Limitation in transpiration by hydraulic conductance and xylem cavitation in *Betula occidentalis.* Plant Cell Environ. 16:279-287.

Sperry, J. S and Ikeda, T. 1997. Xylem cavitation in roots and stems of Douglas-fir and white fir. Tree Physiol. 17:275-280.

Sperry, J. S., Hacke, U. G., Oren, R. and Comstock, J. P., 2002. Water deficits and hydraulic limits to leaf water supply. Plant, Cell Environ. 25:251-263.

Spicer, R. and Gartner, B.L. 2001. The effects of cambial age and position within the stem on specific conductivity in Douglas-fir (*Pseudotsuga menziesii*) sapwood. Trees 15:222-229.

Spittlehouse, D.L., 2002. Sap flow and transpiration of old lodgepole pine trees. Proceedings from 25th Conference on Agricultural and Forest Meteorology, 20-24 May 2002, Norfolk Viginia, American Meteorological Society, Boston MA. pp. 1-8.

Stewart, C.R. 1981. Proline accumulation: Biochemical aspects. In "Physiology and Biochemistry of Drought Resistance in Plants. Academic Press, Sydney, pp 243-259.

Stout, D. and A. Sala. 2003. Xylem vulnerability to cavitation in *Pseudotsuga menziesii* and *Pinus ponderosa* and from contrasting habitats. Tree Physiol. 23:43-50.

Tezara, W. V. J. Mitchel, S.D. Driscoll and D.W. Lawlor, 1999. Water stress inhibits plant photosynthesis by decreasing coupling factor and ATP. Nature 401:914-917.

Tyree, M.., 1989. Co-occurring stress: Drought. Biologic Markers of Air-Pollution Stress and Damage in Forests (1989). Commission on Life Sciences, National Academy of Sciences, 500 fifth street, N.W. Washington DC, 20001, pp.357-363.

Tomlinson, G. H. 1992. A possible mechanism relating increased soil temperature to forest decline. Water, Air, & Soil Pollution; Publisher: Springer Netherlands. 66: numbers 3-4.

Tyree, M.T. and J.S. Sperry, 1998. Do woody plants operate near the point of ctistrophic xylem disfunction caused by dynamic water stress? Answers from a model. Plant Physiol. 88:547-580.

USDA Forest Service, 2006a. Forest Insect and Disease Identification and Management Training Manual, USDA, Forest Service, R-1, Timber, Coop. Forestry and Pest Management, Idaho Department of Lands, Bureau of Private Forestry - Insect and Disease Section, Montana Department of State Lands, Division of Forestry.

Varga, F. 1987. Erkrankung und Absterben der Bäume in den Stieleichenbeständen Ungarns. Österr. Forstz. 98: 57-58. (Cited in: Fuhrer, 1988).

Van Bavel, C.H.M., 1996. Potential evapotranspiration: the combination concept and its experimental verification. Wat. Res. Res. 2:455-467.

Van Bergen, P.F. and I. Poole. 2002. Stable carbon isotopes of wood: a clue to palaeoclimate? Palaeogeography, Paleaoclimatology, Palaeoecology 182:31-45.

Van der Ploeg, M.J., H.P.Ap.Gooren, G. Backer, C.W. Hoogendam, C. Huiskes, G.H. de Rooij, L.K. Koopal, H. Kuridhof, R.A. Feddes, 2005. Measuring soil water potentials with polymer tensiometers. Wageningen University, 6700 HB Wageningen,the Netherlands. http://www.fz-juelich.de/icg/icg-iv/datapool/page/540/Presentatie%20Juelich.pdf.

Vinnedge J., 2004. Notification of Ungulate Winter Range u7-002, Ft. St. James Mule Deer. Forest Ecosystem Biologist, Omineca Region, British Columbia Ministry of Water, Land and Air Protection.

Wackerly, D., W., Mendenhall (III), R. Scheaffer. 2002. Mathematical Statistics with Applications, Sixth Edition. pp. 688-696 and pp. 716 for p-values.

Waring, R.H. and Cleary, B.D. 1967. Plant moisture stress: evaluation by pressure bomb. Science 155:1248-1254.

Wilson, A.T., and M.J. Grinsted. 1977. $^{12}C/^{13}C$ in cellulose and lignin as palaeothermometers. Nature 265:133-135.

Winter K., J.A.M. Holtum, G.E. Edwards and M.H. O'Leary, 1982. Effect of low relative humidity on 13C value in two C3 grasses and in *Panicum milioides*, a C3-C4 intermediate species. J Exp Bot 33: 88–91.

Wilson, B.F. 1984. The Growing Tree. The University of Massachusetts Press: Massachusetts. pp. 55.

Whittaker, C. 1999. The wildlife use and habitat attributes of Douglas-fir in Northern Ecosystems: Structural and functional diversity, (Cited in: Lousier, J.D. and Kessler, W.B., 1999 pp 29-33).

Woodruff, D.R., Bond, B.J. and Meinzer, F.C. 2004. Does turgor limit growth in tall trees? Plant Cell Environ. 27:229-236.

Woodward F.I., 1986. Ecophysiological studies of the shrub *Vaccinium myrtillus* taken from a wide altitudinal range. Oecologia 70: 580–586.